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PALAEONTOLOGY

VOLUME 1 · PART 4

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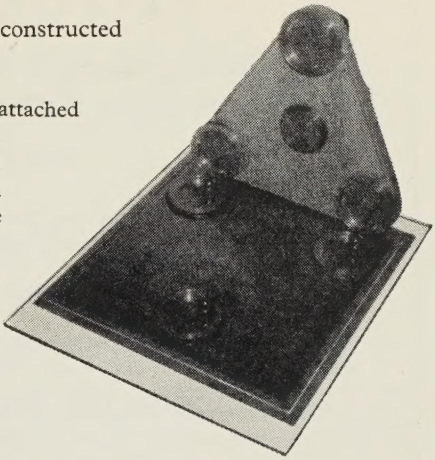

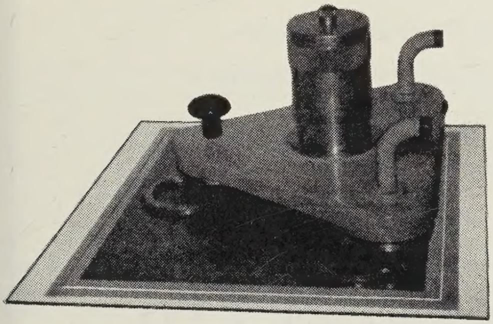

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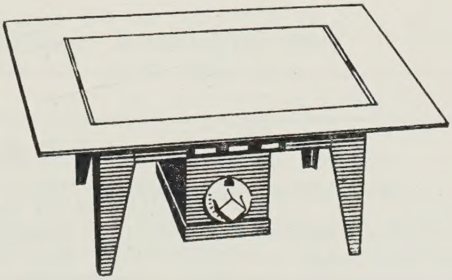

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THE EXTERNAL ANATOMY OF SOME CARBONIFEROUS 'SCORPIONS'
PART 1

by LEONARD J. WILLS

ABSTRACT. The dorsal anatomy of Carboniferous 'scorpions' has long been known to resemble closely that of Recent scorpions, but ventral organs, especially those of respiration, and details of the appendages have rarely been seen. A new technique for separating the chitinous skin from the ironstone in which the fossils commonly occur, has allowed various parts of the exoskeleton to be completely isolated from the matrix, including some of great value in appraising the mode of life of the animals, and some that are used in the systematic classification of Recent scorpions. Often the minutest details have been revealed.

Part 1 describes the technique and discusses our previous knowledge and the classifications that have been propounded. The validity of Pocock's two groups—Lobosterni and Orthosterni—is accepted. The rest of Part 1 relates to two Lobostern 'scorpions'. Revised diagnoses of *Eobuthus sp.*, Wills 1925 (here renamed *Pareobuthus salopiensis* gen. et sp. nov.) and of *Lichnophthalmus pulcher* Petr. are followed by a detailed description of the latter. Certain of the organs found in both genera appear to be adaptations to an aquatic existence. Part 2 will deal with the Orthostern 'scorpions'.

INTRODUCTION AND ACKNOWLEDGEMENTS

CARBONIFEROUS 'scorpions' have always been recognized as scorpions on account of the remarkable similarity of their shape, general organization, and even of the detailed structure of some of their organs to homologous features in Recent forms. Perhaps the most reliable item of all the evidence of their close relationship is the possession of the paired comb-organ or pecten, which has been seen in many specimens. This sense-organ is not known in any other group of Arthropods, though it has been claimed to exist in the doubtfully Eurypterid *Glyptoscorpius*; but I have made a preparation of the teeth of its 'comb', and find them to be devoid of the peg-organs characteristic of the teeth of the scorpion comb, whether fossil or Recent.

With one exception, Carboniferous 'scorpions' have been described from specimens still embedded in the rock, and most of them have been found in ironstone nodules. Usually the plane of the fracture which has exposed the fossil passes along the dorsal surface, bits of the chitinous skin being left on both halves of the nodule. Very rarely have the ventral organs been displayed, and complete appendages have hardly ever been visible or their relation to the body observed. Such minute features as the terminal claws and pedal spurs on the legs and trichobothria on the pedipalpi—features largely employed in classifying Recent forms—are still rare occurrences. For these reasons the fossils have been identified by dorsal characteristics of the grosser type, such as the number of abdominal or post-abdominal segments, the position of the median eyes, the presence or absence of lateral eyes, the length and breadth, &c., but there is often distortion with its consequent difficulty in distinguishing primary and secondary features.

In 1925 I described a number of pieces of the chitinous skin of a crumpled scorpion which I had extracted with a needle and brush from a grey Coal Measures shale (Wills 1925), but the preservation and method of extraction were such that only a few organs

[Palaeontology, Vol. 1, Part 4, 1959, pp. 261–82, pls. 49–50.]

remained in their original relations one to another, and many parts, including the carapace and tail, were never seen. However, the wealth of detail preserved was extraordinary and showed in my opinion that this creature, belonging to the Carboniferous genus *Eobuthus* Fritsch, had, unlike Recent scorpions, no respiratory stigmata, and probably breathed by some sort of gill lying above the overlapping lobes of the sternites. As the dorsal surface of *Eobuthus* is, in every detail, that of a normal scorpion, this discovery implied that it is unsafe to classify a Carboniferous 'scorpion' from its dorsal surface alone—a disconcerting conclusion since this is the usual surface exposed and the one whose characters have almost invariably been used for purposes of identification and classification. I became sceptical about the supposed close similarity of organization of Carboniferous and Recent forms, and especially about the respiratory systems.

Carboniferous 'scorpions' are very rare fossils, but in 1956, with the co-operation of Dr. Isles Strachan, I risked destroying one belonging to the Geology Department of Birmingham University in an attempt to extract from one half of an ironstone nodule the chitinous ventral skin and appendages, the fossil itself being then exposed as an internal mould of the dorsal surface with a few scraps of chitin still attached. My primary objective was to discover how the animal had breathed. Though not entirely successful in this, the results were so remarkable that I was able to persuade Dr. C. J. Stubblefield to allow me to develop three undescribed specimens from the Geological Survey Museum. Later Dr. E. I. White allowed me to treat two specimens belonging to the British Museum. Dr. R. M. C. Eagar provided an undescribed specimen from the Manchester Museum, and Mr. J. T. Wattison of Shrewsbury gave me two halves of an incomplete body of yet another example. I am indebted to these gentlemen for allowing me to try out a new technique on unique specimens at the risk of their destruction. I also thank Professor F. W. Shotton for giving me facilities to work at the Geology Department at Birmingham University, and his laboratory steward, Mr. L. Vaughan, for help with the photography. I wish to thank Mr. A. E. Rixon, chief preparator in the Department of Palaeontology, British Museum (Natural History), for embedding specimens and for advice. To Dr. I. Strachan I am indebted for experimentation, advice, and help in devising the technique and in operating it on the first specimen we treated. I also thank Mr. R. B. Wilson for the loan of specimens from the Geological Survey collection, Edinburgh; and Dr. H. Ball for his help when I have visited the British Museum (Natural History).

The descriptive terms used in the sequel, apart from new ones here defined, are those used by Petrunkevitch (1955, pp. P61–3) or Wills (1947, pp. 3–18). The collections are indicated by initials—B.M., British Museum (Natural History); B.U., Birmingham University, Geology Department; G.S.M., Geological Survey Museum, London; G.S.E., Geological Survey, Edinburgh; M.M., Manchester Museum.

List of abbreviations used in the illustrations. acl, anterior claw; *app*, anterior plate of sternum of pecten; *ats*, anterior tarsal spur; *ap*, anterior process of carapace; *b*, boss on rachis of pecten; *bch*, basal joint of chelicera; *bo*, border; *C XIV–XVIII*, caudal rings of adult segments XIV–XVIII; *c 1–4*, coxae of legs 1–4; *ca*, carapace; *cl*, claw; *cr*, cephalic region of carapace; *d*, dagger; *ebc*, end of broken claw; *et*, eye tubercle; *f*, fulcra; *hch*, hand of chelicera; *hpd*, hand of pedipalp; *L*, left; *L.L. 1–4*, left legs 1–4; *md*, mandibular process of coxa 1 or 2; *me*, median eye; *mg*, median groove of carapace; *mt*, metatarsus; *mts*, metatarsal spur (arising from base of metatarsus); *pcg*, posterior cephalic groove; *pcl*, posterior claw; *pd*, pedipalp; *pe*, pecten; *ppp*, posterior plate of sternum of pecten; *ps*, platform spine; *pts*, posterior tarsal spur; *pVn*, posterior V-notch of sternite; *R*, right; *R.L. 1–4*, right legs *1–4*; *ra*, rachis of pecten; *S IX–XII*, sternites of adult segments IX–XII; *S XIII*, sternal plate of adult segment XIII; *se*, spinule on doublure of sternite; *set*, seta, bristle, movable hair; *spe*, sternum of pecten; *st*, sternum of prosoma; *T VII–XII*, tergites of adult segments VII–XII; *T XIII*, tergal plate of adult segment XIII; *ta*, tarsus; *tas*, tarsal spur; *th*, teeth of pecten; *tr*, thoracic region of carapace.

MODE OF PRESERVATION

The following features in the fossilization of Carboniferous 'scorpions' in ferrous carbonate ironstone—usually a clay ironstone nodule—control my method of extracting their chitinous integument by etching with hot dilute hydrochloric acid. The skins, hairs, setae, &c., are preserved with the chitin virtually unaltered chemically. The sclerites, if intact, retain a considerable degree of flexibility, but in most cases they are broken up by innumerable cracks, sometimes into a mosaic (Pl. 49, figs. 2, 7, 9). Usually, however, the fragments of chitin and occasionally neighbouring sclerites, such as the joints of a leg, are held together by kaolinite (kindly identified by X-ray analysis by Dr. G. F. Claringbull) which appears to have been precipitated as a mass of microcrystals, the distribution of which in the ironstone is always related to the presence of the fossils, whether 'scorpions' or plants. For example, in one case the legs etched out almost intact and flexed as in life as a result of reinforcement of kaolin, the growth of which seems to have burst the cylindrical joints and torn the spines and hairs from them (Pl. 50, fig. 16). In many cases the kaolin fills cavities and thus retains the original shape; for example, each of the little sac-shaped teeth of the 'scorpion's' comb; and in the case of a plant, *Asterophyllites*, it fills the pith cavity of the main stem and its circle of branches at every node (Pl. 50, fig. 17). Still more remarkable is its ability to cover one side of a laminate sclerite, such as a carapace, a tergite, or a sternite, holding the chitin in a thin rigid sheet that retains the original shape and contouring of the sclerite even if its chitin be broken into a mosaic (Pl. 50, figs. 6–8). In the last instance the arrangement again suggests that the fracturing of the chitin may have been the result of the growth of the mass of crystals. When thick the kaolin is opaque, but where thin it may be so translucent that to the eye it hardly obscures the structures that it surrounds.

Other substances insoluble in hot dilute hydrochloric acid are (*a*) crystals of iron pyrites which may be troublesome because they are opaque and usually firmly attached to the chitin or the kaolin; (*b*) coalified fragments of plants—macrospores, seeds, leaves, and stems, which when still in the acid may be mistaken for bits of chitin or, in the case of stems filled with kaolin, may add to the difficulties of extracting the 'scorpion' sclerites; (*c*) detrital clay and some waxy hydrocarbon which together get trapped in the CO_2 bubbles given off during the etch, and form a black oily scum on the hot acid. This floats off as a waxy mass when the preparation is taken from the acid and is immersed in warm water. In this way it is possible to remove nearly all the clay of the clay ironstone that has been released by the solution of the ferrous carbonate at the end of each stage of etching without inverting the specimen and without recourse to washing.

EXTRACTION FROM THE IRONSTONE

The following technique for extracting the chitinous skin has been evolved to some extent by trial and error, and I give it without claiming more than that it is workable with luck and patience.

1. Trim the sides of the specimen if possible so that it becomes roughly rectangular. With waterproof ink rule two lines across the matrix at right angles, and if possible, a third, parallel to and 1 inch from

one of these. Continue these lines as sawcuts on the sides and back of the specimen. The lines should be close to the exposed fossil and parallel to the sides of the specimen if it has been squared up, or to the intended sides of the Marco block in which the fossil is to be embedded. The object of the lines and sawcuts is to enable one to locate the position of anything revealed on the back of the nodule in its correct relation to the original fossil.

2. Examine, photograph under alcohol, and sketch the fossil.

3. Make several enlargements of the photo, ×4, printing one from the front of the negative and several from the back.

4. Prepare a grid of ¼-inch squares on a sheet of celluloid, big enough to cover the whole piece of ironstone and the block of Marco; also a similar grid with 1-inch squares on paper, several copies of which will be needed.

5. Prepare a shallow metal box, big enough to take the specimen easily and deeper than its thickness. Melt a little paraffin wax in it, and on this lay the specimen face upwards as level as possible. Add wax until the lower part of the ironstone is embedded in it. Now mix enough of the transparent polyester plastic Marco (supplied by Scott Bader and Co. Ltd., 109 Kingsway, London, W.C. 2) or similar plastic that polymerizes at room temperature, to fill the space above the wax and to cover the exposed surface of the fossil to a depth of 2–3 mm. Pour this and allow to polymerize. Cement down a glass cover-slip about the same size as the box, using fresh Marco. This glass usually falls away during the etching, but produces a smooth surface through which the specimen may be viewed. If the specimen is deep, pour only enough Marco to give a layer 6 to 8 mm. thick, and allow this to polymerize before pouring another layer. Allow the Marco to stand for two or three days, wipe off any sticky residue and remove the wax.

6. If thought advisable, grind the back of the specimen roughly parallel to the front, in order to reduce the amount of matrix to be dissolved.

7. Heat 10 per cent. HCl in a basin on a water bath and in it place the Marco block and specimen with the exposed surface of ironstone upwards. Etch with pauses to examine the surface until some part—perhaps the claws—begin to appear. The first examinations can be made by lifting the specimen out of the acid and turning upside down in a basin of water to remove the scum and mud, but as soon as any chitinous part appears examination should be made thus: take the specimen carefully out of the acid and, keeping the exposed surface upwards, slide it slowly into a basin of warm water deep enough to cover it easily. The scum of mud floats away, and the specimen is withdrawn slowly, still with the exposed surface upwards. By this time it will probably lie at the bottom of a shallow well surrounded by Marco. If there are delicate parts exposed, the water in this well should be drawn off by a pipette until the ironstone is only moist. The specimen can then be safely carried to the dissecting microscope where water is restored by a pipette and an examination can be made. Never carry the specimen in water enough for loose bits to be washed out of position.

8. Place the ¼-inch celluloid grid over the well and, looking vertically through it, note the position of any object worth recording and sketch in the same on the 1-inch grid (which will ultimately be related to the lines on the exposed surface and the ×4 enlargement printed in reverse). A separate 1-inch grid is needed after each etch, at any rate when much is emerging. It is often advisable to photograph at this stage and print ×4 to supplement one's sketch.

9. Suck off the water again and invert the moist, but not wet, specimen in a basin of water at the bottom of which are one or two 3×1 slides to catch, if possible, anything which has etched loose and any of the matrix which has not floated off with the waxy bubbles. If the specimen was originally thick, the well may now be deep. If so, drill a small drainage hole in the side of the Marco; otherwise air gets trapped in the inverted well. The hole is also useful to drain off the acid before the descumming described in (7).

10. Remove water from the specimen as before, transfer to microscope and re-examine under water. Photograph if necessary and note on 1-inch grid anything that now appears for the first time, having been obscured previously by debris.

11. Manoeuvre any bits of chitin left in the basin on to a 3×1 slip using a pipette or brush or feather. Get the slip out of the water, wash off obvious mineral particles, examine the rest. If possible arrange the bits of chitin as they had appeared in (8). If a piece has to be turned over, always do this under water deep enough to cover the specimen in every position. If unrelated, put each bit on a separate slip. In every case label the slip with the number of the etch and position on the grid or otherwise relate

the mount to the grid (the grids must also bear the number of the etch). Also, if possible, note which aspect is uppermost as mounted.

In some cases a bit first seen in an early etch may not become detached from the matrix until a later etch, and occasionally may remain throughout, being ultimately found to be attached to the Marco-cast.

12. Repeat (7) to (11) until all the matrix has disappeared (in some cases it may be well to stop the etching before this stage has been reached), numbering carefully each etch or group of etches on 1-inch grids, the photos and the mounts. There will then remain the mould in Marco of the parts originally exposed together with any chitin embedded in or attached to it. This, 'the Marco-cast', will now show the ink lines and/or sawcuts made in (1) and it will be possible to relate the grid sketches and progress photos to it and to the reversed ×4 photographs of the original exposed fossil. The Marco must now be thoroughly soaked in water to remove any acid.

13. Cement a cover-slip on to the flat side of the Marco-cast using either Xylol Balsam or Marco to replace the original slip which will almost certainly have flaked off during the etching.

The Marco-cast can now be examined from both sides by reflected or transmitted light, provided that the well has some water or alcohol put into it. It may be advisable to photo the side exposed by the etching.

Finally, in some cases where there is plenty of chitin embedded in the Marco-cast, the well after complete drying may be filled with Marco. After this has set and matured the surface must be ground flat and either polished or covered by a glass slip. When this is done all the skin that was originally exposed in the ironstone together with other bits of skin that have remained attached to the Marco are revealed inside a transparent block.

14. In mounting the pieces remember that the chitin is very delicate and fragile, and must always be moved under water. The bits can be wetted and dried indefinitely. If any piece needs to be turned upside down, do this in water deep enough to cover it in every possible position it may take up. A dodge that sometimes succeeds is to place a 3×1 slip in a shallow basin of water, drain off the water from the specimen, invert it and the slip it is on; then just dip them into the water in the basin, when the specimen may drop on to the waiting slip the right side up.

(*a*) If the specimen is in one piece it can be allowed to dry off under a bell jar to protect it from dust and draughts. When completely dry, damp it with benzol, remove any air bubbles and mount under a cover-slip, using Balsam in Xylol, Euparol, or Marco.

(*b*) If the specimen is broken or consists of several pieces, arrange these in appropriate positions under a film of water. Allow to dry almost completely, run in a little dilute seccotine, allow this to dry completely, damp with benzol, and mount as above. Unless the bits are thus stuck to the slip they float apart during the covering process. On the other hand air may be trapped during the drying of the seccotine, and this mars the final result. This is obviated by using very dilute seccotine.

(*c*) Balsam in Xylol and Euparol are easy to use but have the disadvantage that they take years to dry, especially if the mount is a thick one. Marco, on the other hand, sets completely, but with some contraction which may draw in air bubbles, if any are trapped under the cover-glass. After polymerization it is almost insoluble in any ordinary reagent, so that a remount is virtually impossible, whereas Balsam and Euparol are soluble in benzol and ethyl alcohol respectively, even after a year or more has elapsed.

(*d*) If the specimen is thin it can be mounted in any of the above under a cover-slip without any spacing between the cover-slip and the 3×1 slide; but if it is moderately thick spacing must be provided such as strips of glass or a ring of some sort. Marco is best for both moderately thick and very thick specimens, but it is very mobile before polymerization and a ring of wax should surround the specimen to prevent it flowing out from under the cover-slip. If the specimen is very thick a glass or plastic spacing-ring or washer should be cemented carefully, with no gaps below it, on to the 3×1 glass. When this has set, pour in the Marco to the brim and allow it to polymerize nearly or completely. A meniscus will form on its surface, which should be carefully filled with Marco and covered with a cover-glass, making certain that there is no bubble below the cover. Should one be found, take off the cover-slip, re-fill and re-cover.

CLASSIFICATION

When I began the present study, it appeared to me that Carboniferous 'scorpions', as then known, fell naturally into the two divisions of the order Scorpionida, Latreille 1817

= Scorpiones, Hemprich and Ehrenberg 1826, instituted by Pocock (1911, p. 10) in the following words:

> I propose, therefore, the term Lobosterni for those with bilobed, posteriorly laminate sternal plates on the opisthosoma and skeletal plates, whether belonging to the fourth leg or not, on each side of the genital operculum; and the term Orthosterni for those agreeing apparently with recent scorpions in the structure of the plates in question.

This classification has been rejected by Petrunkevitch (1913, p. 32; 1953, p. 18); but it seemed to me as I read the evidence, that it was valid because the Lobosterni, the dorsal parts of which resemble the homologous organs of terrestrial Recent forms, appeared to possess gills, and were probably aquatic animals. On the other hand, the respiratory organs of the Orthosterni were so imperfectly known that they might or might not have been terrestrial. Despite the absence of convincing evidence, authors were making the assumption that the Orthosterni were terrestrial air-breathers because of their general close resemblance to the scorpions of today which are exclusively terrestrial.

In this connexion the evidence bearing on the question of the mode of respiration is crucial, and should be capable of supplying an item of major diagnostic importance in any ordinal classification. Although Carboniferous 'scorpions' have always been regarded as true scorpions, and in spite of the fact that Petrunkevitch (1955, p. 68), in his latest diagnosis of the Order Scorpionida, has included 'four pairs of book lungs with stigmata on the four sternites following the combs', there has always been some uncertainty as to how the Carboniferous forms breathed. Various authors have claimed to have recognized respiratory stigmata on the surface of the sternites of the adult segments IX–XII (as in Recent forms), but Petrunkevitch after seeing virtually every specimen has rejected all claims but three. Of these he gives (1953, p. 15) unqualified acceptance to one of the two stigmata figured and described by B. N. Peach (1881) as occurring on *Eoscorpius* (now *Archaeoctonus*) *glaber* Peach, and he appears to agree doubtfully that stigmata may be present on *Isobuthus krapulensis* Thorell and Lindström, and on *Cyclophthalmus senior* Corda (Petrunkevitch 1953, pp. 20 and 25 respectively). I have not seen the two Prague fossils, but after very critical examination of Peach's specimens (G.S.E. 5858/9) I cannot convince myself that what has survived of the structures described as 'slit-like spiracles, surrounded with a raised margin' is a stigma. This occurs at the right end of sternite XII in No. 5859, but there is no trace of its opposite number on the same sternite or of any others on sternites IX–XI, all of which are reasonably well exposed.

It is curious that in his recent works Petrunkevitch makes no allusion to the omission by Pocock (1911) from his diagnosis of the Orthosterni of any reference to the absence or presence of stigmata on the unlobed sternites of that group, or to Pocock's comment (1911, p. 15) on the lobed sternites of the Lobostern 'scorpion' *Eobuthus holti* Pocock: 'I can find no trace of stigmata on these sterna; hence I suppose that the respiratory lamellae lay beneath them as they do in *Limulus*'; or to my demonstration (Wills 1925) that stigmata are definitely wanting from the sternites of another species of *Eobuthus*. It would appear that he attaches little importance to the presence or absence of stigmata, at any rate as evidence of habitat, for (1949, p. 134) he wrote: 'The absence of spiracles in fossil scorpions can not be used as evidence of aquatic respiration.'

In the past, attempts have been made to use coxo-sternal features for purposes of classification, but the method breaks down in practice because these parts are so seldom seen, and because, when visible, they can so rarely be related to the dorsal features.

Information about the ventral parts, the mode of preservation, and the detailed structure of the appendages, that has emerged during the present work is described and discussed in the sequel: but even now we are no further advanced in our quest for a workable scheme of classification. The truth is that there are so few specimens of Carboniferous 'scorpions', and these so imperfectly preserved and displayed as they lie in the rock, that any grouping into families, superfamilies, and suborders, cannot be operated in practice, and even the assignment of a new specimen to any of the established genera is often difficult or impossible. The same has now proved to be the case even after dissection by etching.

For these reasons I confine myself in this paper to describing the details of the anatomy revealed in nine specimens by the extraction of the chitinous skin from the rock. These dissections have shown some remarkable similarities in the structure of certain organs to their homologues in Recent forms, particularly in the family Buthidae. But they have also shown that homologous organs were sometimes developed on lines unknown amongst Recent scorpions.

In view of the above the only classification here attempted is into (*a*) the groups Lobosterni and Orthosterni of Pocock; (*b*) genera (*s.l.*); and (*c*) species.

LOBOSTERNI Pocock 1911

PAREOBUTHUS gen. nov.

Type species *P. salopiensis* sp. nov.

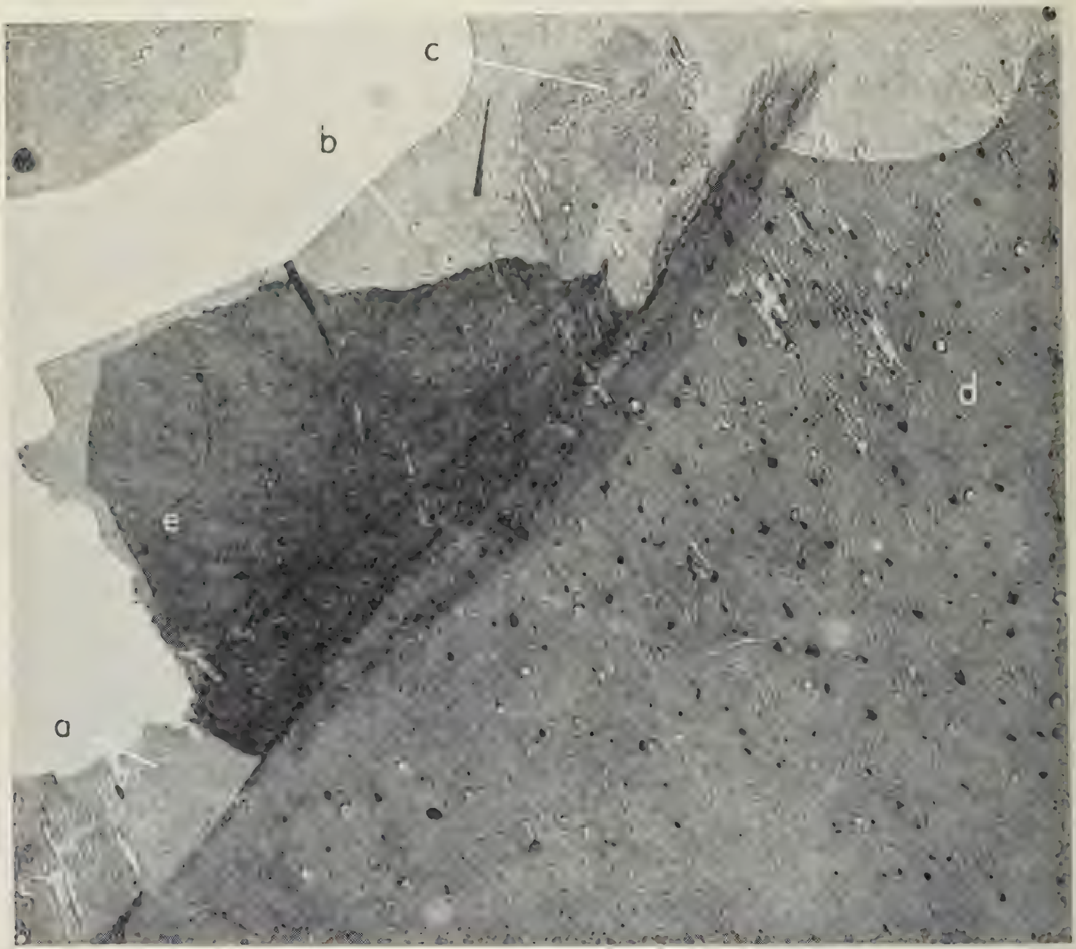
The type species of this genus was described in 1925 as *Eobuthus sp.* (Wills 1925). Since then the genus *Eobuthus* Fritsch has been stated by Petrunkevitch (1953, p. 18), after seeing all Fritsch's types, to be congeneric with *Isobuthus* Fritsch. As my specimen agrees closely as regards the coxo-sternal arrangement and the shape of the sternites with the type-specimen of *Eobuthus rakovicensis* Fritsch in Prague and the paratype in the British Museum, but differs from *Isobuthus krapulensis* Fritsch as regards the terminal claws on the leg and the supposed respiratory stigmata of *Isobuthus* (queried as such by Petrunkevitch 1953, p. 19), and as we are ignorant of the claws of *Eobuthus*, I am erecting a new genus and species for my specimen.

Pareobuthus salopiensis sp. nov.

Eobuthus sp. Wills 1925, pp. 87–97, pl. 3.

Holotype. G.S.M. 87231; Coal Measures, Upper *Anthraconaia modiolaris* zone, probably near to Main Coal of North Wales coalfield; Preesgweene Colliery, Weston Rhyn, Shropshire.

Revised diagnosis of genus and species (with references in brackets to the figures on pl. 3 of Wills 1925). Large scorpion, carapace unknown, tergites 15 mm. wide [fig. 14], with many setae; strongly marked mucronate posterior margins. Chelicera and pedipalp unknown except for fragments; one, ? part of chelicera with supposed stridulation organ [fig. 8]; one, ? part of pedipalp hand with large trichobothria [fig. 18]. Coxae 1 and 2 unknown. Sternum hexagonal, longer than wide with an anterior extension of folded thin skin carrying thick-set setae, coxa 3 abuts against the sternum. Coxa 4, not much longer than coxa 3, abuts against the bilobed genital operculum. ? Sternum of pecten [fig. 11] with a posterior median notch. Pecten (only fragments) with rachis covered with numerous movable setae, many fulcra and teeth, each having sensory field of peg-organs as in Recent scorpions [figs. 4, 6, 7, 10]. Sternite IX unknown, sternites X, XI, XII large, laminate, strongly bilobed behind and with anterior margin with a median notch [figs. 2, 12, 13]. Anterior border with many small setae. These sternites devoid of stigmata, outer surfaces covered with short setae [fig. 16], the posterior lobes with deep flap-like doublure covered with triangular spinules [fig. 16], pointing backwards. Where doublure joined the anterior edge of the next sternite behind, skin very thin and covered with minute hairs [fig. 9]. These three features are refigured on text-fig. 1.



TEXT-FIG. 1. *Parcobuthus salopiensis* sp. nov. Part of sternite X. × c. 75. See Wills 1925, pl. 3, figs. 2, 16. *a*, outer skin showing cellular texture and pore canals; *b*, ditto with scattered hair-bases and one seta; *c*, ditto covered by a sheet of tenuous chitin with minute down hairs (probably part of sternite XI); *d*, outer skin covered by the doublure carrying minute triangular spinules; *e*, dark area due to superposition and plications of the three sheets.

Legs and tail unknown except as numerous fragments. One of these (Wills 1925, text-fig. 3A) shows the tarsalia of a leg, with metatarsus with one strong and one weak row of spines on ribs and many setae; two tarsal spurs, one large with a spinelet and hairs, one small and trifid (cf. *Lichnophthalmus*, p. 270); tarsus half the length of metatarsus, with one spiny rib, a few setae and a rounded claw-lobe; claws (one only preserved) curved, with spiny teeth on inner side and a bunch of setae near tip, the claw-pad (*Gehstachel*) developed as a short 'dagger' (see p. 280). Only one pair of spines and one claw are visible in the specimen, but in view of my discoveries in *Lichnophthalmus* they can be included in the diagnosis with assurance. Birula (1926) identified the 'dagger' as a *Gehstachel* or claw-pad, but advanced a different explanation of the platform-spines. His views are quoted by Werner (1934, p. 35).

LICHNOPHTHALMUS Petrunkevitch 1949

Lichnophthalmus pulcher Petrunkevitch

Plates 49 and 50

Lichnophthalmus pulcher Petrunkevitch 1949, pp. 142, 147, pl. 45, fig. 139; pl. 55, fig. 177.

Material. Holotype B.M. In. 39772, collected by W. Eltringham: Middle Coal Measures, Upper *Anthraconaia modiolaris* zone, Crow Coal; Phoenix Brickworks, Crawcrook, near Ryton-on-Tyne, Co. Durham. Topotype (here described) B.M. In. 39770. Also G.S.M. Za 2842 (Pl. 49, fig. 11), Coal Measures, *modiolaris* zone, Dodworth, near Barnsley, Yorkshire.

Original diagnosis. 'Carapace high, considerably wider than long, and wider behind than in front (fig. 139). A pair of elliptical eyes on a transverse tubercle situated close to anterior edge. Cephalic portion of carapace extends almost to posterior edge.'

Remarks. Petrunkevitch placed this genus in the family Eoscorpionidae. Only the carapace is preserved in the holotype. The eyes are on the sides of an elevated tubercle and I consider that Petrunkevitch is mistaken in claiming them as elliptical. When viewed from the side each is as nearly round as can be expected in a specimen preserved in strong relief. Apart from this debatable feature the carapace can be matched closely with that of the new specimen B.M. In. 39770, and also with G.S.M. Za 2842 to which Petrunkevitch attached a label '? *Lichnophthalmus*'.

Revised diagnosis. Large scorpion, body wider in proportion to length than in a normal Recent form. *Dorsal Prosoma.* Carapace tapers toward front from *c.* 15 to *c.* 12 mm. wide, *c.* 11 mm. long. Cephalic portion V-shaped, elevated, and overhanging a slight median anterior projection, slopes down at sides to flat thoracic portions; a median groove from posterior margin forks anteriorly to embrace an elevated eye-tubercle carrying two large median circular eyes at front. ? Eye-ridges on antero-lateral corners of cephalic part, but lateral eyes not recognizable. On carapace fairly numerous granules without any obvious arrangement. *Dorsal Mesosoma.* Tergites normal, *c.* 15–16 mm. wide, length increasing backwards from *c.* 1·25 to *c.* 3·5 mm.; posterior margins slightly mucronate. *Metasoma.* Dorsal and ventral plates of segment XIII poorly preserved, but ventral plate with large granules. Caudal rings and sting unknown. *Ventral Prosoma.* Chelicera: hand large with hooked fingers: pedipalp—only part of one hand with a finger known, finger long, narrow, hooked distally. Sternum and its relation to coxae unknown. Legs imperfectly known—coxa 1 and/or 2 probably with small narrow mandibular processes. Coxae 3 and 4 long, their relation to the genital operculum unknown.

Tarsalia distinctive, metatarsus, where known, with two spiny ribs and large, rather blunt spines at distal end: two tarsal spurs, one very long and leaf-like, and one shorter with a few spines and hairs seen on 2nd leg, and two of about equal size on 4th leg: Tarsus of 2nd leg almost as long as metatarsus: each tarsus with median claw-lobe: the terminal claw-member on each leg consists of a pair of large toothed claws with a few hairs at distal ends, a large median claw-pad or *Gehstachel* below (here termed a 'dagger') with on either side two spines (here termed 'platform spines') near its base or on skin connecting the pad to the base of the claws: the dagger on 1st and 2nd leg as long as or longer than the claws, but on 3rd leg shorter, and on 4th leg quite small. *Ventral Mesosoma.* There is some uncertainty about the interpretation of the genital operculum and sternum of the pecten. Genital operculum unknown; sternum of pecten composite—a large anterior sclerite and two pairs of posterior sclerites, the outer members carrying the combs. Each comb large, triangular with its rachis only distinct proximally from its middle lamella: distal end of comb studded with thickened bosses carrying sensory setae: 30–35 fulcra and same number of teeth. Sternite IX very thin skinned, outline unknown. Sternites X, XI, XII lamellate with posterior margins bilobed, each widely overlaps the next sternite behind like the lamellate appendages of *Limulus*: doublure of the lobed part with minute spinules.

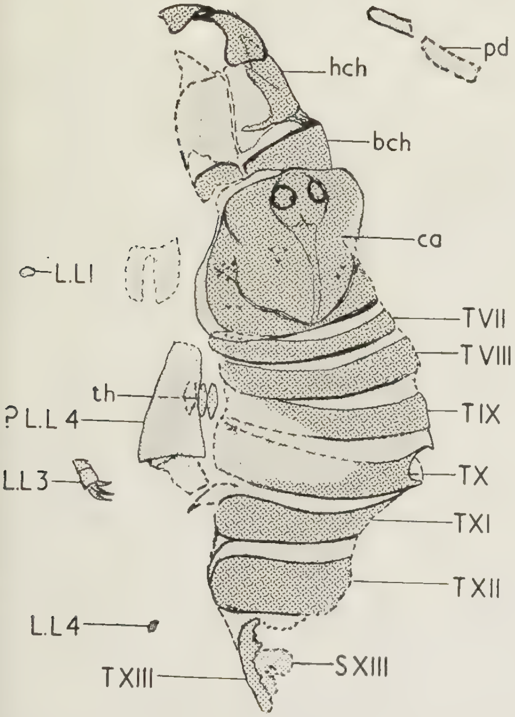
Description of Topotype, B.M. In. 39770

This had been broken into four pieces and mended with glue, which I dissolved in order to examine parts previously invisible under the front of the carapace. After mending with seccotine and after photography it was embedded in Marco and developed on the lines described above. Two of the main cracks had passed through the carapace and coxo-sternal area, adversely affecting the extraction of those parts; on the other hand the reinforcement by kaolin of the sternites, the left comb, and the tarsalia enabled them to retain their original relief and shape, which can now be studied in the Marco-cast and in the mounted preparations. The dorsal skin had fractured during fossilization into a complex mosaic of chitin, but this remained embedded in the Marco-cast where it can still be examined by transmitted light. The dorsal skin has an obvious cellular texture.

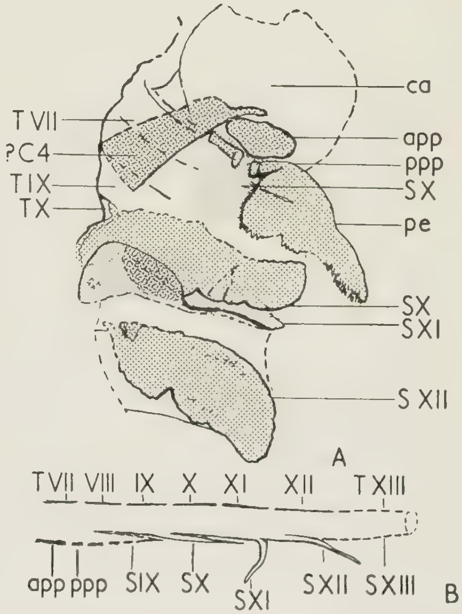
Apart from some crushing and fracture, the dorsal side of the body is well preserved (Pl. 49, figs. 1–3). It lies somewhat twisted, fully distended and strongly arched transversely. Judging from the postures of the sternites and from the distribution of mud on their surfaces—usually on the ventral side but on the dorsal when a posterior lobe is bent forward and inverted—I think that the animal was entombed on its back. From the front of the carapace to the back of the last mesosomatic tergite it measures *c.* 31 mm.; whereas the sum of the sagittal lengths of the carapace and six tergites, as defined by their margins, is *c.* 24 mm. The difference of 7 mm. shows the amount of distension which is taken up by wide strips of structureless intersegmental skin (Pl. 49, fig. 3; text-fig. 2).

Dorsal surface

The carapace. The left side of this is barely distorted and shows the original relief, but the right side has been crushed downwards. It has also been broken and damaged by one of the fractures mentioned above. As defined by its linear margins the carapace measures *c.* 11 mm. in length and is 15 mm. wide behind, but tapers somewhat to the front which appears to have a slight median projection. The cephalic part is strongly elevated so that it overhangs at the front and drops away towards the flatter posterior lateral thoracic portions behind along two slopes that meet behind in a V, from which runs forward a median groove that forks to either side of the eye-tubercle. This bears two median eyes. The left one is circular in outline, but the other appears ellipsoidal as a result of crushing. This right eye thus agrees with those described by Petrunkevitch in the holotype (1949, p. 147), which appear to me to owe their supposed elliptical shape to a similar accident of preservation. In the present specimen it can be seen that the median eyes are formed of dark structureless chitin. In this respect they compare closely with the eyes of Triassic and Recent scorpions (Wills 1947, p. 6). The rest of the carapace has the same remarkable cellular or 'honey-comb' texture as that found in the dorsal skin of *Pareobuthus salopiensis* gen. et sp. nov. (Wills 1925, pl. 3, fig. 17). The antero-lateral corners of the cephalic elevation have ridges that may represent eye-ridges, but no lateral eyes can be recognized on them. On the carapace there is a small number of



TEXT-FIG. 2



TEXT-FIG. 3

TEXT-FIG. 2. *Lichnophthalmus pulcher* Petr. Dorsal aspect, as originally exposed and finally developed. Carapace and tergites separated by wide strips of intersegmental skin (cf. Pl. 49, fig. 1). ×2. For key to abbreviations see p. 262.

TEXT-FIG. 3. *Lichnophthalmus pulcher* Petr. A. Ventral aspect of mesosoma, as far as known, in relation to dorsal elements (cf. Pl. 49, fig. 4). Based on the Marco-cast, progress photos and slides 14, right coxa; 26, left pecten; 21, part (deeply shaded) of S. XI; 20, all of S. XII, right pecten omitted. ×2. B. Section to show postures of sternites and their relation to tergites. For key to abbreviations see p. 262.

largish granules, but their distribution is irregular and different from the arrangement as described in the holotype. The sides and the back of the carapace are defined by a thick linear margin, outside which is a border of thinner skin that at the front end appears originally to have been bent under as a doublure, but now lies in front of the carapace proper, giving an appearance of a blunt median process. That there was also a small median process of the shield itself is likely, since one is clearly seen in Za 2842 (Pl. 49, fig. 10).

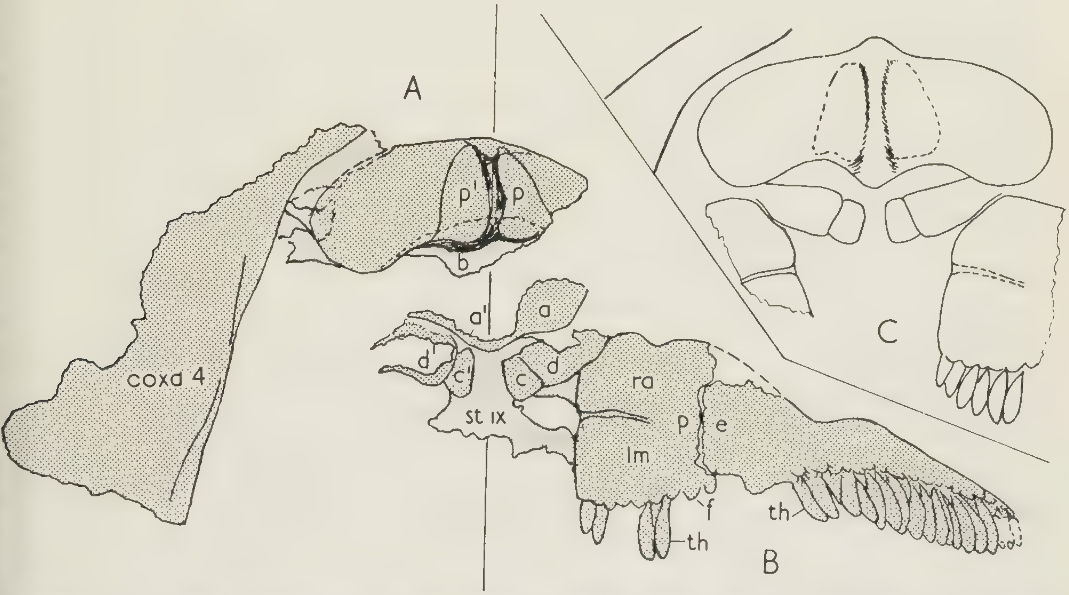
The mesosomatic tergites. The tergites are each bounded by a linear anterior and a thicker, almost mucronate posterior margin which unite at the ends. They carry a few granules on cellular chitin like that of the carapace. The tergites are separated from the latter and from one another by thin intersegmental skin, and from the sternites by thin pleural skin. They measure up to 15 or 16 mm. in width and increase backwards in length (as defined by the margins) from *c.* 1·25 to *c.* 3·5 mm. The first metasomatic tergal plate (segment XIII) is poorly preserved: so too is the corresponding ventral plate, but this showed largish granules on the surviving fragment. The caudal rings and sting were missing.

The sternal region of the ventral surface. The *prosomatic sternum* has not been recognized and the coxae of the legs were only seen as fragments. Their relation to the sternum, so important a feature in classification, could not therefore be determined.

The *genital operculum* is probably missing, but it may possibly be represented by a large plate here ascribed to the sternum of the pecten (see below). Were this plate to turn out to be the operculum, the 4th coxa, which lies along its side but does not abut against it (slide 14; Pl. 50, fig. 5, *app*, and text-fig. 4 C), would occupy a position unlike that which it holds in *Pareobuthus* (Wills 1925, pl. 3, fig. 3) and in all the genera—*Isobuthus*, *Eobuthus*, *Microlabis*, and *Palaeobuthus*—which Petrunkevitch (1955, p. P77) places in his superfamily Isobuthoidea and family Isobuthidae.

The *sternum of the pecten*. Owing to the excessive thinness and fragile nature of the skin of the ventral surface which has led to fracturing and crumpling and to the relative displacement of the more heavily chitinized sclerites, and owing to the partial and irregular flattening of once-curved surfaces, it has proved extremely difficult to reconstruct the sternum of the pecten from the parts that have survived. These are drawn as accurately as possible in text-fig. 4 A, B, based on slides 14 and 26 (Pl. 50, fig. 5 and Pl. 49, fig. 9 respectively). A tentative reconstruction is offered in text-fig. 4 C.

On the present interpretation the sternum or sternal element of the pecten is composite, consisting of five sclerites—a large anterior unpaired plate and four posterior plates, two on either side of the mid-line. The *anterior plate*. More than half of the anterior plate is preserved in relief in slide 14. It appears to be roughly arcuate with median processes fore and aft. Along the mid-line there is an external median rib with a narrow keel. Internally this structure forms a deep groove. On either side of the rib are bulging patches of skin that have remained intact during fossilization, whereas the lateral parts of the plate are of darker chitin that has been broken into a mosaic. The rib has been crushed over towards the left, thus producing an appearance of asymmetry in the specimen. The posterior edge of the anterior plate is bent inwards as a doublure, as are also the two ends of the median rib. The part marked *b* on text-fig. 4 A has probably been displaced, being, I suspect, a portion of this doublure and not a bit of another sclerite, as at first sight it might appear to be. The part of slide 26 marked *a′* on text-fig. 4 A can best be interpreted as a portion of the body-wall which lay immediately above the central part of the posterior doublure of the anterior plate, and that marked *a* as part of its dark-skinned postero-lateral wing. This correlation allows the positioning of the anterior plate in relation to the two pairs of posterior plates on slide 26 (text-fig. 4 B, *c*, *d*, *c′*, *d′*) adopted in the reconstruction (text-fig. 4 C), in which allowances have been made for the irregular crumpling of the excessively thin skin that lies between the various more heavily chitinized sclerites and provided flexible joints between them.



TEXT-FIG. 4. *Lichnophthalmus pulcher* Petr. Ventral view and reconstruction of the region of the pecten. A. Slide 14, coxa 4 and supposed ant. plate of sternum of pecten with *b*, ? doublure, *pp′*, areas of uniform skin separated by an external ridge. B. Slide 26, *aa′*, supposed lat. and med. parts of ant. plate of sternum of pecten; *cc′ dd′*, post. plates of same, St. IX, sternite IX; lettering on L. pecten as elsewhere. The bend in ant. edge is probably due to a fold. ×5. C. Reconstruction of the sternal region. For key to abbreviations see p. 262.

The *posterior plates*. Virtually the whole of the four posterior sternal plates with the left comb still attached to the left outer plate was extracted almost intact (slide 26, Pl. 49, figs. 8, 9; text-fig. 4 B). Their probable relation to the supposed anterior plate has just been argued, but whether that interpretation be correct or not, there is no room for doubt that the four posterior plates are the sternal element which actually carried the combs. They comprise: (*a*) an inner pair (text-fig. 4 B, *c*, *c′*), each being a slight boss of thickish chitin, longer than wide, and separated one from another by a fairly wide median strip of thin skin that spreads out behind into a large sheet which reaches to the lamella of the comb (text-fig. 4 B, *lm*), and which may have merged behind into sternite IX; (*b*) an outer pair (text-fig. 4 B, *d*, *d′*), each being a slight boss, wider than long and slanting obliquely forwards and outwards. To the outer side of the left unit is hinged the rachis (text-fig. 4 B, *ra*) of the left comb by a narrow strip of thin skin. Part of the right unit is also preserved. Each unit of the outer pair can perhaps be interpreted as a basal joint of the comb appendage now fused to the body-wall, the rest being lamellate and freely movable. The discovery of the thin skin attached to both rachis and lamella, and extending between them, emphasizes the high degree of movement and flexibility that the comb possessed. It also explains why the comb has so often been observed displaced or detached from the body of fossil 'scorpions'.

The compound sternal element of the present pecten compares closely with that in *Eobuthus holti* as figured by Pocock (1911, fig. 1), in which, however, only two posterior plates are shown. The subdivision of the posterior plates—clearly seen in the preparation (slide 14)—may well be undetectable in Pocock's type-specimen. Unfortunately this point cannot be verified since the present whereabouts of the Holt collection to which it belongs, is unknown. However, in one, No. 30247, of the four fragments (G.S.M. 30245–8) of the paratype, which Pocock omitted to figure, the five sclerites are clearly displayed, though the specimen does not show the relation of the broad anterior plate to the genital operculum as does the holotype. It is interesting to find that Fritch (1904, pl. 8, fig. 1), in his drawing of the underside of *Eobuthus rakovicensis*, also shows the sternum of the pecten with a wide anterior plate and a posterior unpaired plate, but omits the latter from his reconstruction (1904, text-fig. 92).

The pecten, comb, or comb-organ. This is a paired sensory appendage attached to the second mesosomatic segment (adult segment VIII). In the present case it is a triangular lamellate structure, wide at the proximal end and tapering gradually to the free end.

The left comb attached to the posterior sternal element was extracted virtually intact, thanks to a reinforcement of kaolin (slide 26; Pl. 49, figs. 8–10), and a large part of the right comb, in which the chitin in the absence of reinforcement was still flexible, after flapping about in the acid during several etching stages, was also recovered (slides 25, 28, 29; Pl. 50, fig. 1). Both combs lost many of the teeth, some of which were retrieved (slides 27, 30–36). The whole organ was thus revealed. It comprises:

(*a*) The rachis (text-fig. 4 B, *ra*), and (*b*) the middle lamella (*lm*) which are only distinct at the proximal end, where they are separated by a narrow strip of thin skin (see above) over a distance of about one-sixth of the length of the whole comb. In the more distal part there is a number of areoles outlined by thinner skin and provided in many cases with largish hair-bases to which movable setae were attached (some are still in place) (Pl. 50, fig. 1). These areoles appear to have been slight swellings. They compare closely with the ornament of 'irregular embossed scale-like pattern' figured by B. N. Peach (1881, pl. 22, figs. 3, 3*a*–*c*, pl. 23, figs. 16, 16*a* for '*Eoscorpius euglyptus*', and pl. 23, figs. 8*d*, 8*e* for '*Eoscorpius tuberculatus*'). The whole comb closely resembles that of the former species in size, shape, and structure. Similar areoles occur in *Pareobuthus salopiensis* (Wills 1925, pl. 3, fig. 4).

(*c*) The fulcra (text-fig. 4 B, *f*). The protuberant areoles are exaggerated along the hinder edge of the comb into some 30–35 bag-like structures—the fulcra—which form a continuous row from end to end of it, even in the proximal part where there are no areoles. Each fulcrum carried three or four short sensory setae (several are still in place) attached to conspicuous hair-bases (Pl. 50, fig. 1). In this respect the fulcra resemble those on *Pareobuthus* (Wills 1925, pl. 3, figs. 4, 6) and those on some of the 'scorpions' described in the sequel. The arrangement persists in Recent forms (Werner 1934, fig. 60).

(*d*) Teeth. Alternating with the fulcra were some 30–35 teeth (text-fig. 4 B, *th*) of which 21 survive on slide 26 and 3 still lie in the Marco-cast. They are spindle-shaped bags which in their present crushed state appear to overlap one another obliquely like the 'splints of a venetian blind' (Peach 1881, p. 399). Each tooth has one side plain and the other side, which faces toward the mid-line of the animal, covered with minute peg-organs, each a tiny pit of thin skin with a central peg or papilla (shown in plan and profile in Pl. 50, figs. 2, 3). Some of the teeth show exceptionally clearly these features which appear to be common to all scorpions, whether fossil or Recent (Wills 1925, pl. 3, fig. 10 for *Pareobuthus*, and the second part of this paper for other examples of Carboniferous forms; Wills 1947, pl. 11, fig. 3 for the Triassic *Mesophonus*, and Werner 1934, figs. 60, 62, 63, for Recent forms). A unique feature is seen, however, on the two teeth surviving at the proximal end of the left comb (slide 26; Pl. 49, fig. 9). This is a number of the finest imaginable 'cats-whiskers' clustered round the tips (Pl. 50, fig. 4).

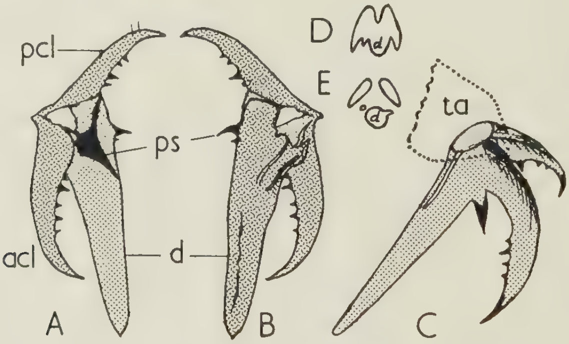
Sternites of the adult mesosomatic segments IX–XII

Sternite IX. This appears to be represented by the largish spread of very thin skin lying behind the posterior plates of the sternum of the pecten (slide 26; Pl. 49, fig. 9; text-fig. 4 B), but this is only a fragment undefined by any margin at the side or behind. The corresponding sternite in *Pareobuthus salopiensis* differs from the other sternites, and in *Eobuthus holti* is a wide flat plate, but here again the posterior margin is not preserved in the fragment of the paratype (G.S.M. 30247), which Pocock did not figure. He shows it with a straight posterior margin in his drawing of the holotype (Pocock 1911, fig. 1).

Sternites X, XI, XII etched out in full relief, being supported by films of kaolin covered with mud on one surface and with a mosaic of chitin on the other. Sternite X still lies adherent to the Marco-cast, and sternite XI stands in the cast with its distal part vertical to the Marco on its left side, and turned right over towards the head on its right side, thus displaying its dorsal-facing doublure to a ventral view. Part of the inverted lobe broke away, but was retrieved as slide 21 (Pl. 50, fig. 6). Sternite XII lay, ventral side up at a lesser, but quite considerable angle. The whole of this sternite broke loose and was mounted as slide 20 (Pl. 50, figs. 7, 8). The postures of both XI and XII imply that the sternites were really overlapping lamellate appendage-like structures. They are shown in Pl. 49, fig. 4 as they appeared at the last stage of etching before sternite XII became detached. The photo is supplemented by text-fig. 3 A, B, in which certain plates of Marco, formed where it had penetrated minute cracks, are omitted. These are responsible for some of the dark shadows on the photo. The text-figure also makes clear the relation of the sternites to the pecten and also to the carapace and tergites.

The general structure of all these sternites appears to be similar. Each is lamellate, about half as long as wide, with its posterior side bilobed and capable of overlapping a good part of the next sternite behind. This implies the existence of a deep doublure forming the ventral wall of the intervening pouch.

The two detached pieces (slides 20 and 21) and another fragment (slide 22) are semi-transparent and can be studied by transmitted light. The external skin, other than the doublure, is fairly thick, dark in colour, and broken into the usual mosaic. Nowhere on this is there any sign of respiratory stigmata. These observations can be checked on Pl. 50, figs. 6–8. Visible through the external skin of sternite XI (slide 21) are minute V-shaped spinules. Some were seen on the inverted part of this sternite during the etching. Obviously spinules are external organs. Here they must have been attached to the doublure and must have been directed towards the pouch. But in slide 21 I can see only one layer of chitin and that is the dark external skin. The explanation of the apparent absence of the doublure-skin would appear to be either that this was extremely tenuous and was not preserved, or that it was pressed against the outer dark chitin before this was broken into its mosaic and is now indistinguishable from it.



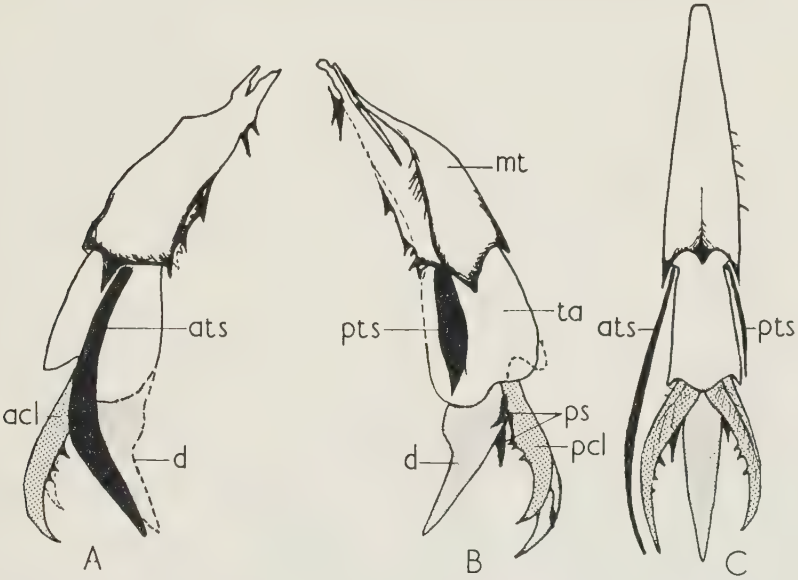
TEXT-FIG. 5. *Lichnophthalmus pulcher* Petr. Claws, platform spines and dagger of supposed left leg 1 (slide 4), × *c.* 10. The larger claw (*acl*) and larger platform spine (*ps*) are anterior. A, dagger below; B, dagger above; C, restoration in perspective, ant.-lat. aspect, showing relation to the tarsus (*ta*); D, E, diagram sections, D at base of claws, E more distally where claws, platform spine, and dagger have separated. For key to abbreviations see p. 262.

On sternite XII (slide 20) two groups of spinules can be seen when the sclerite is viewed from its internal side (Pl. 50, fig. 7) where the skin is unobscured by the muddy kaolin reinforcement (Pl. 50, fig. 8). The group at the anterior end may lie on the external surface in the part that was overlapped by sternite XI. Those at the posterior end doubtless lay on the now invisible doublure of sternite XII, just as do those on sternite XI described above. Both sets of spinules are so minute that their exact relation to the film of chitin cannot be determined with the highest powered objective that can be used. They appear, however, to be closely comparable in shape and distribution with those which I described in the matrix-free preparation of *P. salopiensis*. Here it was possible to demonstrate that they lie pointing backwards on the doublure, which is there visible, though very thin (Wills 1925, pl. 3, figs. 2, 9, 11–13, 16 and present text-fig. 1).

The function of the spinules is unknown, but may have been to exclude solid particles from the pouch. It is interesting to find that similarly shaped but much larger spinules have been found by Waterston (1957, p. 279, pl. 11, fig. 6) on the doublure of an abdominal appendage of an unidentified Eurypterid.

The postures in which these three sternites lie (text-fig. 3 B) demonstrate that their lobate hinder parts were capable of covering gills lying within the pouches formed by the overlap of one sternite across the front of the next one behind. As Pocock (1911, p. 15) points out in his description of *Eobuthus holti*, such an arrangement is comparable with the gill-bearing laminate appendages of *Limulus* which is an aquatic animal (see also Wills 1925, pp. 94–96).

The present evidence is perhaps insufficient to allow us to decide whether or not the Carboniferous Lobostern 'scorpions' carried gills and were aquatic or breathed air by some unknown mechanism—for they certainly possessed no stigmata comparable to those characterizing the true terrestrial scorpions, whether Triassic or Recent. It must be stressed, however, that *Pareobuthus* and the present specimen, which alone have so far permitted a detailed study of their ventral surfaces, have both demonstrated conclusively that the sternites are completely different from those of Recent scorpions and that their organization is more comparable with an aquatic than an aerial mode of respiration.



TEXT-FIG. 6. *Lichnophthalmus pulcher* Petr. Metatarsus with spines and setae, tarsus with large ant. and small post. tarsal spurs, claws with platform spines and dagger, parts of the supposed right leg 2 (slide 3). A, ant. view; B, post. view; C, restoration view from above. × *c*. 10. For key to abbreviations see p. 262.

Appendages

In front of the carapace were exposed parts of the chelicerae. During repairs to the specimen the latter were seen to extend under the carapace. Part of the hand of the right pedipalp lay unnoticed on the surface of the ironstone about 1 cm. away from the shield (Pl. 49, fig. 1; text-fig. 1). Other originally exposed bits of chitin were, during development, found to be tarsalia of legs. As already noted the coxae proved to be missing, imperfect, or so crushed together as to be indecipherable with accuracy. Only fragments were extracted (slide 16). Apart from the supposed trochanter of the 4th leg (slide 13) the joints of the legs intermediate between the coxae and the tarsalia were all missing, lost in the counterpart which has not been preserved.

Chelicera (Pl. 49, fig. 5; text-fig. 2). Parts of the two hands of the chelicerae were exposed on the surface. They are separated from the carapace by two large sclerites which I originally took to be the coxae of the pedipalp. During repairs to the specimen (p. 270), these were found to extend under the front of the carapace. The one on the right side lies in the Marco-cast, and can, I believe, be seen to be connected by thin skin to the hand. For this reason it must be interpreted as the basal joint of the chelicera. If this be correct, the whole chelicera is abnormally large, in fact, longer than the whole carapace. Among fossil 'scorpions' this proportion is approached in *Microlabis sternbergi* Corda as figured by Petrunkevitch (1953, fig. 21). Here they are about three-quarters the length of the carapace.

The fingers of the right hand etched out well (Pl. 49, fig. 5), but unfortunately they were damaged in mounting, and now only the single-pointed tip of the supposed fixed finger with its bristles can be satisfactorily viewed (slide 9). Before it was damaged, the sturdy, movable finger (Pl. 49, fig. 5) carried a bunch of forwardly-directed bristles, and was, I believe, bifid at its distal end. With its point almost interlocking with this bifid finger, lay the tip of the single pointed finger mentioned above.

Apart from their size the supposed parts of the chelicera resemble in organization and relative proportions the homologous units of this appendage in Recent scorpions and in the Carboniferous 'scorpions' to be described in the second part of this paper (Geological Survey Museum No. Za 2926).

Pedipalp (Pl. 49, figs. 6, 7; text-fig. 2 *pd*). Crushed bits of the coxae were extracted (slide 16) but nothing definite can be deciphered. Of the apparently long narrow hand, part still adheres to the Marco-cast and part was extracted (slides 10 and 11). Slide 10 preserves about 11 mm. of the distal end of one of the fingers (Pl. 49, fig. 6). It is hooked slightly at its end and is thickly covered throughout its length and on both sides by long setae with occasional still larger ones. There is a dense cluster of rather short slender hairs at the tip. Other details are obscured by matrix; but as a whole, it compares closely with the fixed finger of the Survey specimen Za 2926 to be described in the sequel. The latter has, however, lost all the setae.

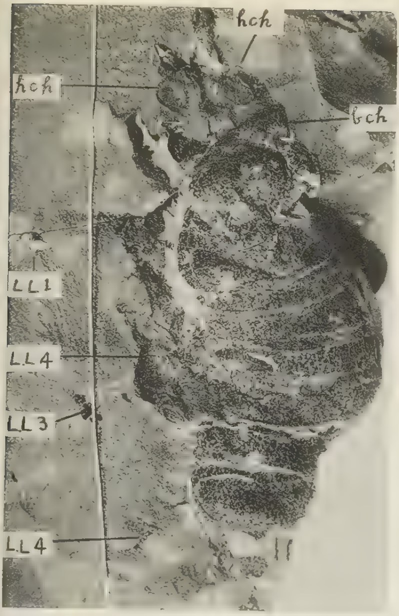
The legs. As already noted the coxae were poorly preserved. Probably coxae 1 and 2

EXPLANATION OF PLATE 49

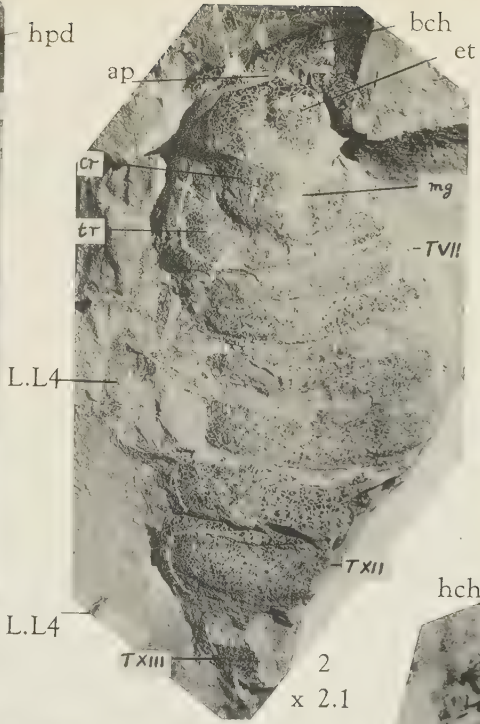
For key to abbreviations see p. 262.

Figs. 1–9. *Lichnophthalmus pulcher* Petr. Crow Coal, Middle Coal Measures, Crawcrook, Ryton-on-Tyne, Co. Durham. B.M. In. 39770. 1, Dorsal view of whole specimen as originally exposed, cf. text-fig. 1. ×1·7. 2, Carapace and abdomen photoed under alcohol. Dark flakes are chitin as mosaic in kaolin. ×2·1. 3, Cephalic region of carapace viewed from in front. ×2·1. 4, Ventral view of body after etching and before sternite XII fell away. Sternites outlined, cf. text-fig. 2. ×1·7. 5, Ventral view of free finger with bristles, and tip of ? fixed finger of right chelicera, and supposed mandibular process of coxa 1 or 2. ×5. 6, Ventral view of finger on right pedipalp (slide 10). ×4·6. 7, Ditto, distal end to show hairs (slide 10). ×17. 8, Ventral view of left pecten attached to its sternal plates, cf. text-fig. 3. Chitin reinforced by kaolin (slide 26). ×4·2. 9, Ventral view of tip of left pecten before extraction. ×6·3.

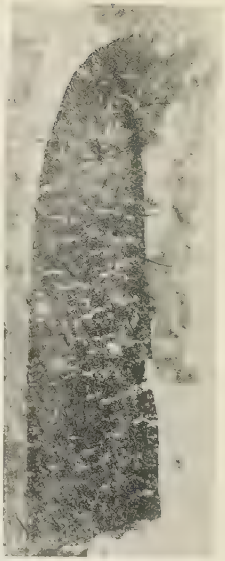
Fig. 10. *Lichnophthalmus pulcher*? Petr. Parkgate Coal, *modiolaris* zone, Dodworth, Barnsley, Yorks. G.S.M. Za 2842. Flattened carapace in shale showing ant. process, circular median eyes and granules. ×4·2.



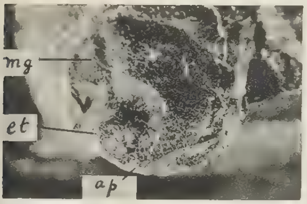
1 x 1.7



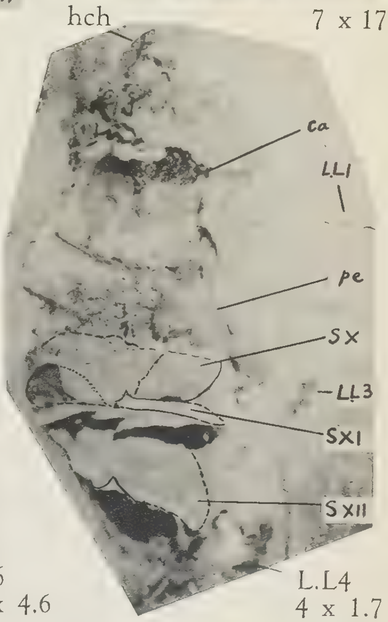
2 x 2.1



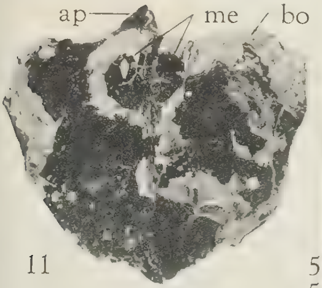
7 x 17



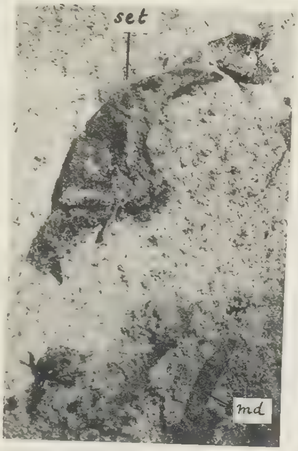
3 x 2.1



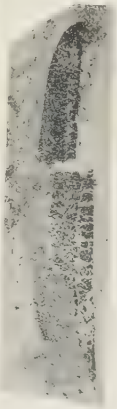
4 x 1.7



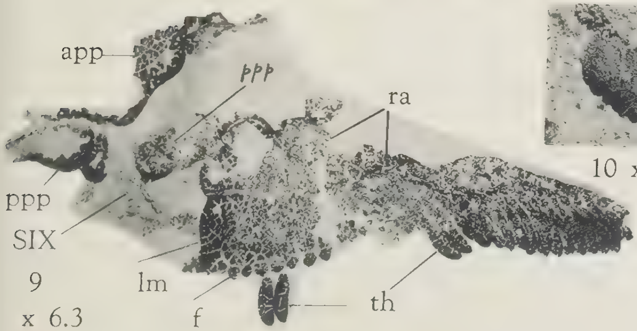
11



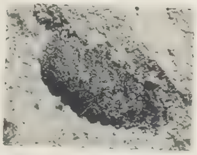
5 x 5



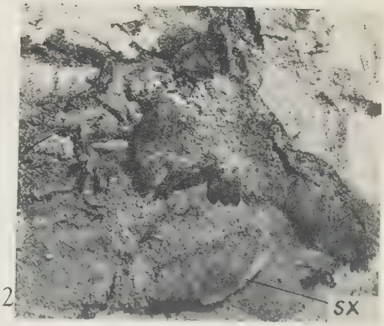
6 x 4.6



9 x 6.3



10 x 4.2

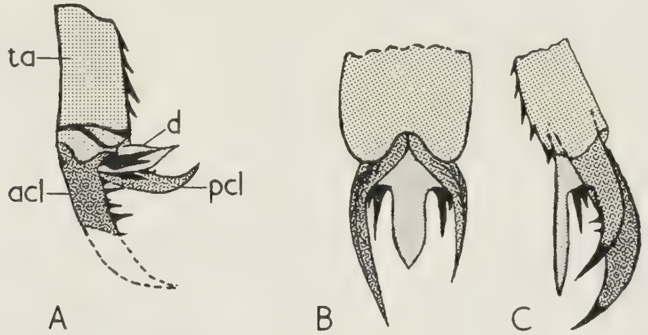


8 x 4.2

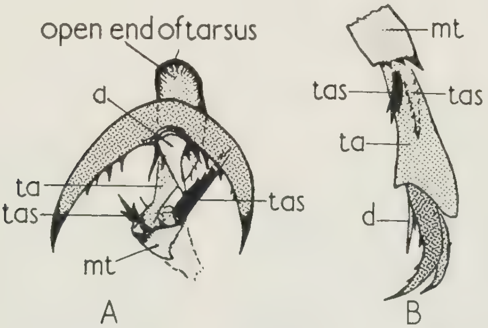
WILLS, Carboniferous "Scorpions"

each had a small, narrow, hairy mandibular process. One is shown on Pl. 49, fig. 5. Coxae 3 and 4 are represented by fragments, but were probably long, rather narrow cylinders, coxa 4 lying alongside the sternum of the pecten (Pl. 50, fig. 5). A possible trochanter 4 is mounted on slide 13.

The joints of the legs intermediate between the above and the tarsalia are missing. Hence there is some doubt about which of the four legs carried each of the four types of tarsalia discovered. The following attributions are therefore tentative. The terminal claws and their pads (*Gehstacheln*) have a unique design which varies in detail from leg to leg (Pl. 50, figs. 9–15; text-figs. 5–8). The arrangement consists of a pair of curved claws, toothed on their inner sides with, between their bases, a remarkable modification of the pad, for the skin connecting the inner bases of the two claws forms a kind of platform from which project: (*a*) a large central 'dagger' as long as or even longer than



TEXT-FIG. 7. *Lichnophthalmus pulcher* Petr. A. Incomplete tarsus, claws with 2 pairs of platform spines and dagger, parts of the supposed right leg 3 (slide 1). Ant. view, × *c.* 10. B, C, restorations; B, view from above; C, view from behind to show the 'platform' of dagger and platform spines lying below the claws, and joined to their inner sides. For key to abbreviations see p. 262.



TEXT-FIG. 8. *Lichnophthalmus pulcher* Petr. A. Incomplete metatarsus and tarsus with tarsal spurs, all nearly vertical and capped by horizontally splayed-out claws with platform spines and short dagger forming a platform below the claws. Right leg 4, as etched out, × *c.* 7: owing to the posture and crushing, the relative sizes of the parts are only approximate. B. Restoration. For key to abbreviations see p. 262.

the claws in the supposed legs 1 and 2, but only half as long or less in the supposed legs 3 and 4; (*b*) one or two smaller sharp spines on either side of the dagger. These 'platform spines' project from the edge of the platform except on the supposed leg 1, where they are outgrowths of the dagger.

The details are difficult to decipher but can best be seen in the 2nd and 3rd legs (slides 3 and 1) in which the tarsalia lie on their sides. In slide 3 both sides can be examined. In other cases the claws had splayed out and one can see that they lie on a different plane from that of the platform. In the text-figures I have attempted accurate sketches of what can be seen, together with reconstructions of the original arrangement before the parts were crushed or flattened.

Supposed 1st leg. Slide 4; Pl. 50, figs. 9, 10; text-fig. 5. The largest dagger is on the supposed 1st leg. It is quite a startling organ on account of its length (3 mm.) and robustness. It is perfectly preserved even to two narrow strips of thin skin, like elastic sides to a boot, which can be seen on one side, serving to give flexibility to the joint. Near the base of the latter, on either side, are a pair of platform spines, one large and one small, but there is no real platform. The two claws of unequal size are splayed out, approximately equal in length, and armed on their inner sides, the smaller with four and the larger with five teeth. They carried a few setae near their sharp, curved ends. Though the dagger and claws were at first attached to the tarsus, they broke away during the etching. The tarsus and two largish tarsal spurs were later extracted (slide 5), but it is impossible to reconstruct them in detail.

Supposed 2nd leg. Slide 3; Pl. 50, figs. 11, 12; text-fig. 6. On this leg the dagger is likewise about as long as the claws (one of these was broken across in mounting but its

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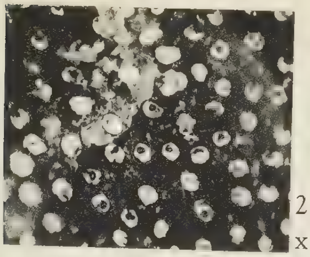
EXPLANATION OF PLATE 50

For key to abbreviations see p. 262.

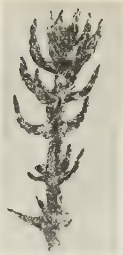
Figs. 1–15. *Lichnophthalmus pulcher* Petr. Crow Coal, Middle Coal Measures, Crawcrook, Ryton-on-Tyne, Co. Durham. B.M. In. 39770. 1, Ventral view of right pecten preserved in transparent chitin (slide 25). ×14. 2, Peg organs on a tooth of the pecten, in plan (slide 32). ×255. 3, The same in profile (slide 32). ×*c*. 500. 4, 'Cat's whiskers' on the tip of one of the two proximal teeth of left pecten showing on Pl. 49, fig. 8 (slide 26). ×125. 5, Dorsal view of supposed anterior plate of sternum of the pecten, and part of right coxa 4 (slide 14). ×6·6. 6, Detached piece of the overturned lobe of sternite XI, showing spinules (slide 21). ×10·3. 7, Dorsal concave aspect of two-thirds of sternite XII, showing chitin mosaic on kaolin (slide 20). ×4·1. 8, Ventral convex aspect of the same (fig. 7), showing muddy kaolin obscuring the chitin mosaic (slide 20). ×4·1. 9, 10, Claws, dagger, and platform spines of supposed left leg 1: 9 from below, 10 from above (slide 4). ×9. 11, 12, Metatarsus, tarsus, claws and dagger of supposed right leg 2 (slide 3). 11 from behind (ventral as found) shows short metatarsal spur, 12 from in front (dorsal as found) showing long leaf-like tarsal spur ×8·2. 13, Tarsus, claws, and dagger of supposed right leg 3 (slide 1). ×6·2. 14, The same of supposed left leg 3, still attached to Marco-cast. ×5. 15, Claws splayed out on top of crushed tarsus of supposed left leg 4, photoed when still attached to Marco-cast (note the shadow). ×*c*. 2·5. 15*a*, ? hand of the chelicera and ? mandibular processes of leg 1 or 2. ×4.

Fig. 16. ? *Buthiscorpius buthiformis* Pocock. B.U. 720. Metatarsus of left leg 3 showing the dark chitinous skin separated by white kaolin from the setae that once lined its side (slide 720/a). ×25.

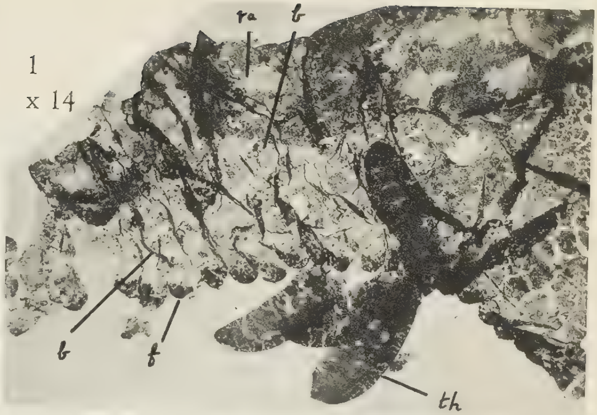
Fig. 17. *Asterophyllites sp*. A plant preserved in its original shape by a kaolin infilling of its pith cavities. G.S.M. 87232, extracted from G.S.M. Za 2924, below Top Hard Coal, Shipley Clay Pit, near Ilkeston, Derbyshire. ×5·2.



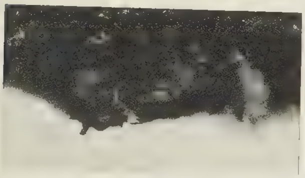
2
x 255



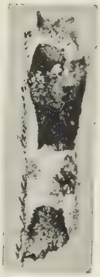
17 x 5.2



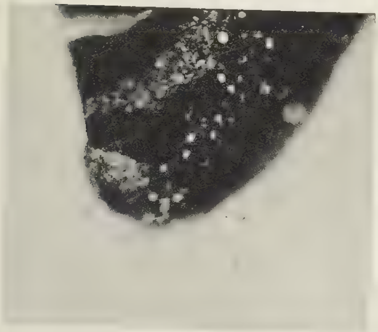
1
x 14



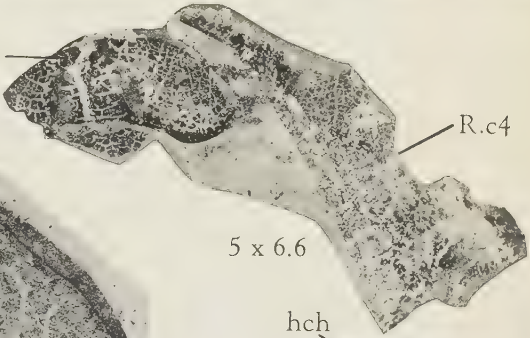
3
x c.500



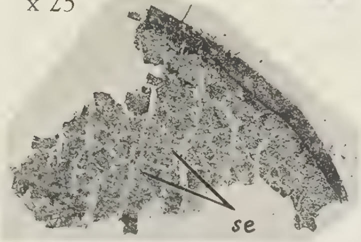
16
x 25



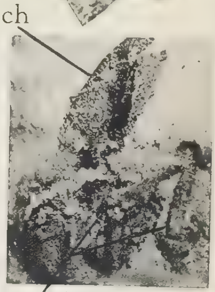
4 x 125



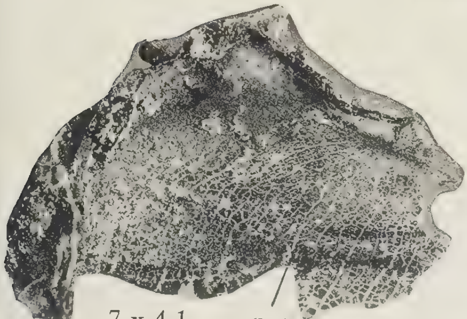
5 x 6.6



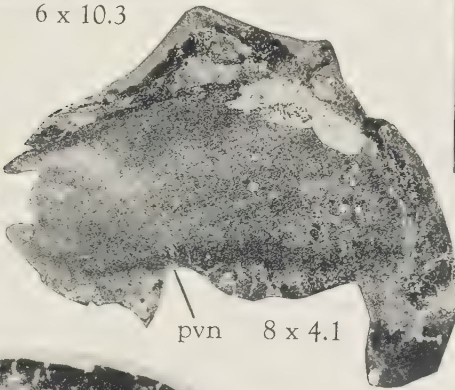
6 x 10.3



15a x 4

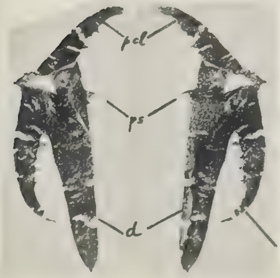


7 x 4.1

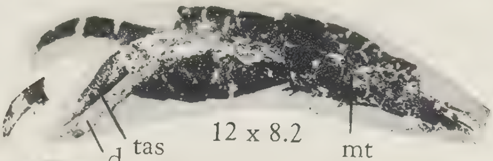


8 x 4.1

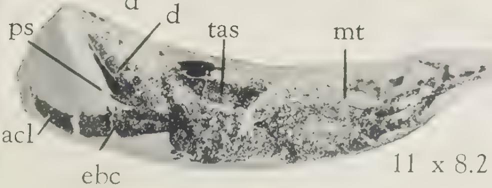
15
x c.2.5



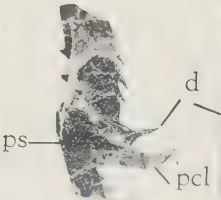
9 x 9   10 x 9



12 x 8.2



11 x 8.2



13 x 6.2

14 x 5

distal end lies adjacent on the slide). There are large spines near the bases of the claws and dagger, one apparently part of the claw, and the other attached to the dagger, as in the supposed 1st leg. The platform is absent or reduced.

The relationship of the claws and dagger to the short, but rather thick tarsus is clearly seen. The tarsus does not show any marked keels or spines, but above the claws the claw-lobe is well developed. At the base of the tarsus are two modified tarsal spurs; one is about half the length of the tarsus and has a sharp end and a few spines along one side; the other is remarkable for its length, for it extends almost to the ends of the claws as a narrow leaf-like structure, clearly flexible and unarmed in any way. It would appear to be an organ useful to an aquatic animal but not to a dweller on land.

The metatarsus is seen on slide 3 to be strongly keeled, with spines along the keels and large ones at their distal ends. At its proximal end the metatarsus is obscured on one side by what may be a metatarsal spur (if so, this is probably the 3rd leg, not the 2nd).

Perhaps part of the tibia of this leg is preserved in slide 6, but details cannot be deciphered and it is not known for certain that this specimen came from the base of the metatarsus in slide 3. A sketch made during development suggests that it did.

Supposed 3rd leg. Pl. 50, figs. 13, 14; text-fig. 7. The tarsalia of both of the 3rd legs were found: one lay at the extreme hind end of the specimen and was mounted as slide 1, the other is still attached to the Marco-cast. The structure is well seen in slide 1. The claws are slightly unequal, the larger has five or six spiny teeth, the smaller three. The dagger is short, leaf-shaped, and ends in a sharp spine. On the skin which unites the dagger to the base of the claws on either side, lies a pair of sharp platform spines: the inner spine of each pair is nearly as long as the dagger, the outer being much shorter. Most of the above features can also be seen in the other example (Pl. 50, fig. 14).

The claw parts are attached in both cases to a rather stout tarsus with a spinose keel on its lower side and a claw-lobe on its upper. A few hairs are also visible. In the example still in the Marco can be seen the very spiny end of the metatarsus and one tarsal spur about half as long as the tarsus. It has a spinelet near its tip and carries several hairs. Probably there was originally a second tarsal spur, which has been lost: consequently it is impossible to say whether this limb carried a long spur like that preserved in the supposed 2nd leg.

Supposed 4th leg. Pl. 50, fig. 15; text-fig. 8. Until the finish of the etching the end of this leg still projected upwards from the Marco. Unfortunately the claws finally broke away and were lost, leaving only bits of the tarsus and metatarsus and two large bristles still attached to the Marco. However, I had previously photographed it, made the drawings, and written the following description.

The tarsalia were difficult to decipher as a result of their standing up 2 or 3 mm. like a pillar crushed from above, parts of which were overshadowed by the claws. These facts make uncertain the remarks about the relative sizes and shapes of the different parts.

The claws each carrying four teeth were splayed out flat, with the platform lying at a lower level, but centrally between their bases. The dagger was a short sharp spine, approximately one-third of the length of the claws. It was flanked on either side by a pair of smaller platform spines of unequal size. Level with the claws was the open end of the tarsus which stood nearly vertically and was thus difficult to examine, but it could be seen to taper downwards to the place where it entered the spine-girt open end of the metatarsus. At this point were two tarsal spurs. One showed only its trifid end, but appeared to be short, the other had spinelets down one side and may have been longer.

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PLIOSAURUS BRACHYSPONDYLUS (OWEN) FROM THE KIMERIDGE CLAY

by L. B. TARLO

ABSTRACT. The associated skeleton of a Pliosaur from the Kimeridge Clay of Ely is described. Since it is the first known Pliosaur of Kimeridgian age which possesses both mandible and limb girdles associated with the vertebral column, it provides a means whereby Kimeridgian Pliosaurs can be separated into two distinct groups. On the characters of its mandible and scapula the Ely specimen is placed in the genus *Pliosaurus*, while the characters of its cervical vertebrae enable it to be included in the species *P. brachyspondylus* (Owen).

INTRODUCTION

HITHERTO it has been impossible to do more than suggest from circumstantial evidence that there were two distinct groups of Pliosaurs in Kimeridgian times. The known remains fall into two groups on the characters of the mandible, and also into two groups on those of the scapula. No associated skeleton has yet been described in which both mandible and scapula are present, and it has therefore not been possible to say with any certainty what the relationship was between the groups based on mandibles and those based on scapulae.

The two associated skeletons known, *Pliosaurus brachydeirus* and *Pliosaurus macromerus*, both lack essential parts. In *P. macromerus* the pectoral girdle, but no mandible, is known, whereas in *P. brachydeirus* the mandible is preserved but there is no pectoral girdle. A type of mandible different from that of *P. brachydeirus*, and a type of scapula different from that of *P. macromerus*, are also known, but as these are all from isolated specimens they could not be assigned to definite species.

This problem has now been resolved. In the Sedgwick Museum, Cambridge, there is a mandible and vertebral column of a Pliosaur from the Kimeridge Clay of Ely (J. 35991) which, although collected in 1889, has never been identified or described. Along the length of the ventral surface of the vertebral column are fragments of the limb girdles, forming a long narrow strip of broken and somewhat distorted bone 150 mm. wide. This mass, except for the vertebrae themselves, has been difficult to interpret, but a careful examination has now revealed the presence of the left scapula and coracoid. This scapula is of the same kind as the isolated scapulae mentioned above, which are quite different from that of *P. macromerus* (see Tarlo 1958*b*); further, the mandible agrees almost exactly with that of the type of *P. brachydeirus*.

This means that the isolated scapulae can now be linked with the mandible of the *brachydeirus* type, leaving the isolated mandibles to be assigned to *P. macromerus*.

HISTORY OF THE SPECIES

Conybeare (1824*a*) figured four Pliosaur vertebrae from the Kimeridge Clay of Weymouth which were then housed in the Collection of the Philosophical Society of Bristol. Later (1824*b*) he proposed the name *Plesiosaurus giganteus* for Plesiosaurians with shortened neck vertebrae, and included the centra from Weymouth in this species.

[Palaeontology, Vol. 1, Part 4, 1959, pp. 283–91, pls. 51–52.]

Owen (1839) also described such shortened cervical vertebrae from the Kimeridge Clay of Heddington Pits, near Oxford, and he proposed the name *Plesiosaurus brachyspondylus* for them. He also used this name to cover the vertebrae from Weymouth. In his description of the cervical vertebrae from the Heddington Pits, Owen noted that the 'articular surfaces are very slightly concave, with small round depression, but no convex rising at the centre. The sides and underpart of the body are concave [i.e. from anterior to posterior, L. B. T.], the surface is tolerably smooth.'

The specimens from Heddington were in the collection of Viscount Cole (later Earl of Enniskillen), the greater part of which is in the British Museum. Unfortunately none of the vertebrae can now be traced, and Woodward and Sherborn (1890) could not locate the type material. Also I have been unable to find the Weymouth vertebrae.

The only author to discuss the species *Plesiosaurus brachyspondylus* was Seeley (1869), who correctly assigned it to *Pliosaurus*. Seeley listed and described a late cervical vertebra, with which thirty dorsal vertebrae were associated, from the Kimeridge Clay of Roswell Pit near Ely, Cambridgeshire. His description agrees with Owen's and it seems that the Heddington and Roswell specimens were conspecific. The posterior ('late') cervical centrum from Roswell (now in the Sedgwick Museum, Cambridge) is thus the only specimen of *P. brachyspondylus* (Owen) mentioned in the literature which is still extant. It should be noted that in 1871 Phillips described and figured several Plesiosaur vertebrae, incorrectly assigning them to *Plesiosaurus brachyspondylus* Owen.

In 1889 an associated Pliosaur skeleton was collected from the Kimeridge Clay of Ely and the characters of its posterior cervical vertebrae are identical to those of Seeley's Roswell cervical centrum. It appears that it is specifically identical to *P. brachyspondylus*, the types of which are now lost. In view of this I feel there is a good case for erecting a neotype, and I shall make the requisite application for the late cervical centrum described by Seeley to be so considered.

SYSTEMATIC PALAEONTOLOGY

Family PLIOSAURIDAE Seeley 1874

Genus PLIOSAURUS Owen 1841

Type species *Pliosaurus brachydeirus* Owen 1841

Diagnosis. Mandible with long symphysis bearing 10–12 teeth of which the anterior 5–6 are large and caniniform; total of 30–38 teeth in each ramus. Cervical vertebrae short, length about half width or height; cervical ribs double-headed. Scapula triradiate with dorsal process directed laterally and ventral plate expanded medially; coracoid elongated with postero-lateral expansion; ischia elongated; propodials long, compressed dorso-ventrally, expanded distally; epipodials short.

Pliosaurus brachyspondylus (Owen)

Plates 51 and 52

Plesiosaurus giganteus Conybeare 1824*b*, p. 389.
Plesiosaurus brachyspondylus Owen 1839, pp. 78–80.
Pliosaurus brachyspondylus (Owen), Seeley 1896, pp. 97, 102–4.
Pliosaurus brachyspondylus (Owen), Lydekker 1889, pp. 139–40.
Non *Plesiosaurus brachyspondylus* Phillips 1871.

Diagnosis. Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae with double rugosity and without ventral keel; posterior cervical vertebrae without boss in centre of articular surfaces.

Neotype (here proposed). J. 29564, Sedgwick Museum, Cambridge, posterior cervical centrum, Kimeridge Clay, Ely, Cambridgeshire, described Seeley 1869, pp. 97, 103.

Other material. G. 102, Dorset County Museum, anterior cervical centrum, Kimeridge Clay, Osmington, Dorset; J. 47225, Sedgwick Museum, Cambridge, anterior cervical centrum, Kimeridge Clay, Chettisham, near Ely, Cambridgeshire; J. 35991, Sedgwick Museum, Cambridge, associated skeleton, Kimeridge Clay, Ely, Cambridgeshire, described in present paper.

DESCRIPTION OF NEOTYPE

The posterior cervical centrum described by Seeley (1869) and now in the Sedgwick Museum (J. 29564) is chosen as the neotype of *Pliosaurus brachyspondylus* (Owen). It is here figured for the first time (Pl. 51, figs. 1, 1*a*–*c*). This vertebra is very distinctive since it possesses a double rib facet on the left side and a single facet on the right.

The articular surfaces of the vertebra are transversely ovate in outline, and are slightly concave. Each has a small depression at its centre, there being no suggestion of any convexity developed such as is the case in the posterior cervical vertebrae of other Kimeridgian Pliosaur species. The margins of the articular surfaces are very sharply defined, and there is no evidence of either a marginal bevel or groove.

On the ventral surface of the centrum are two nutritive foramina, and the surface itself is convex between the rib facets. On the anterior and posterior margins of this ventral surface are two strips of finely sculptured rugose bone between which the surface is remarkably smooth. This last feature is very striking and can readily be used to distinguish the species.

	Measurements (in mm.)		
	Length	*Height*	*Width*
Centrum	36	68	79
Left superior rib facet . . .	24	27	. .
Left inferior rib facet . . .	20	15	. .
Right rib facet	25	33	. .

DESCRIPTION OF ASSOCIATED SKELETON FROM ELY

In 1889 and 1890, Mr. H. Keeping, the collector of the Woodwardian (now Sedgwick) Museum, brought to the Museum an associated Pliosaur skeleton, now catalogued under J. 35991.

This specimen consisted of numerous teeth; the complete mandible; the greater part of the vertebral column; two limb bones, and fragments of limb girdles, many of which had been preserved in natural articulation with the vertebral column cemented on top of them.

The bulk of the vertebral column is preserved in two blocks, the larger of which (Block A) contains fragments of the skull, the posterior half of the cervical vertebrae and the anterior half of the dorsal vertebrae (see Pl. 52, figs. 1, 1*a*). Part of the left scapula and the lateral half of the left coracoid adhere to the ventral surface of these vertebrae. The second block (Block B) consists of eight dorsal centra, with several abdominal ribs and part of the pubis preserved on their ventral surface.

The atlas, axis, and the two cervical vertebrae following them are preserved in association with the mandible. In addition, there are some isolated fragments of bone, including the symphysial regions of both coracoids, the left one of which fits on to the glenoid part of the coracoid which adheres to the ventral surface of the dorsal vertebrae. Part of an ischium is present as an isolated bone, as are also the right humerus and left femur.

TEETH. The teeth are similar to those of *Pliosaurus brachydeirus* Owen in that they are trihedral in cross-section; the enamel of the flat outer surface is smooth but the remainder of the crown is characterized by longitudinal ridges (see Pl. 51, figs. 3, 3*a*). This type of tooth is common to all Pliosaurs of Kimeridgian age and thus cannot be used to distinguish the different species of that age from one another (Tarlo 1958*a*).

MANDIBLE. The separate elements of the mandible are all preserved, but it is somewhat difficult to distinguish between sutures and post-mortem effects due to the process of fossilization. The total length of the mandible is 1,200 mm. The symphysis is 328 mm. in length and 128 mm. at its greatest width. It contains ten teeth on each side, of which the anterior six are large and caniniform. The fourth, fifth, and sixth teeth are the largest, and the mandible is expanded to accommodate them, but it becomes constricted at the seventh tooth which is markedly smaller than the three previous teeth. There is a total of thirty teeth in the right ramus and thirty-one in the left (see Pl. 51, fig. 2).

This specimen is similar in shape to the mandible of *P. brachydeirus* in which there is also an elongated mandibular symphysis containing ten to twelve teeth of which the anterior five to six are large and caniniform. In consequence I consider this specimen to be generically identical to *P. brachydeirus*, the type species.

VERTEBRAL COLUMN. A total of forty-five vertebrae are known, of which nineteen are cervical, two pectoral, and twenty-four dorsal. Since many of these centra are preserved in natural articulation it is an easy task to determine their serial position. The length of

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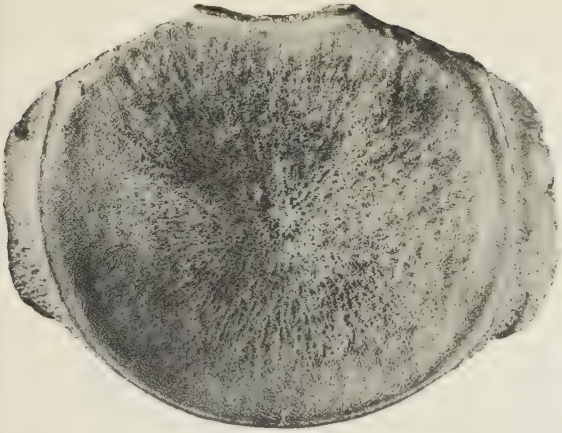
EXPLANATION OF PLATE 51

Figs. 1–5. *Pliosaurus brachyspondylus* (Owen), Kimeridge Clay, Ely, Cambridgeshire. Figs. 1, 1*a–c*, J. 29564, Sedgk. Mus., Cambridge, posterior cervical centrum here proposed as neotype. 1, Anterior view; 1*a*, Ventral view showing finely-sculptured rugose strips; 1*b*, Lateral view of right side showing single-rib facet; 1*c*, Lateral view of left side showing double-rib facet, approx. ×1. Figs. 2–5. J. 35991, Sedgk. Mus. 2, Mandible in dorsal view showing long mandibular symphysis, ×⅛. 3, 3*a*, Tooth, 3, External view; 3*a*, Lateral view, ×1. 4, Block B in ventral view showing dorsal vertebrae, abdominal ribs, and part of pubis, ×⅛. 5, Left femur in dorsal view, ×⅛.

EXPLANATION OF PLATE 52

Figs. 1–2. *P. brachyspondylus* (Owen), Kimeridge Clay, Ely, J. 35991, Sedgk. Mus., Cambridge. 1, Block A in ventral view showing cervical vertebrae, left scapula, and lateral half of left coracoid; 1*a*, Dorsal view showing squamosal, cervical, pectoral, and dorsal vertebrae, also dorsal process of left scapula; 1*b*, Atlas and axis with 3rd and 4th cervical centra, ×⅙. 2, Fragment of limb girdle showing chitinous hooks from the tentacles of cephalopods, which must have formed a major part of the food of the animal, ×1.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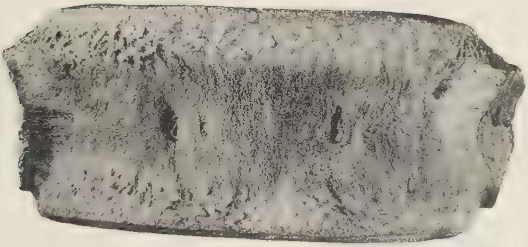
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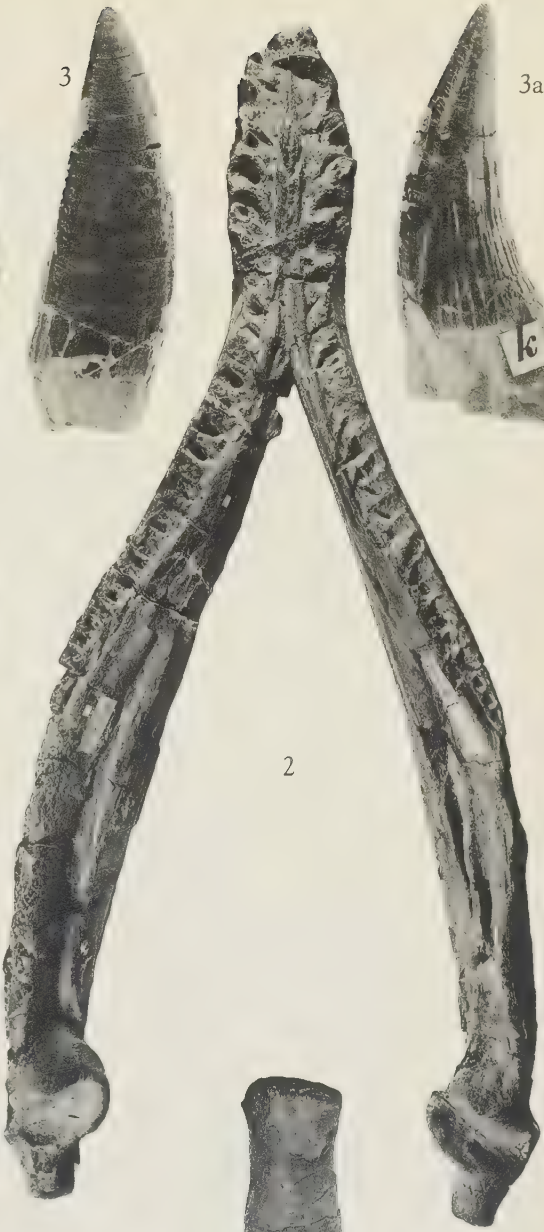
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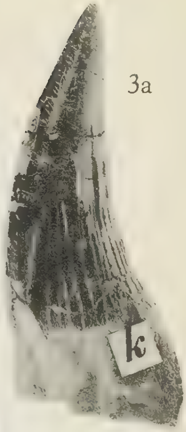

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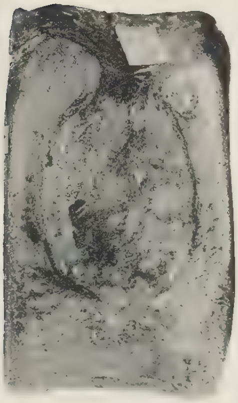
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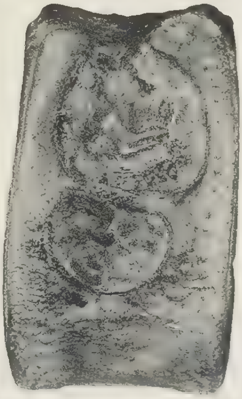
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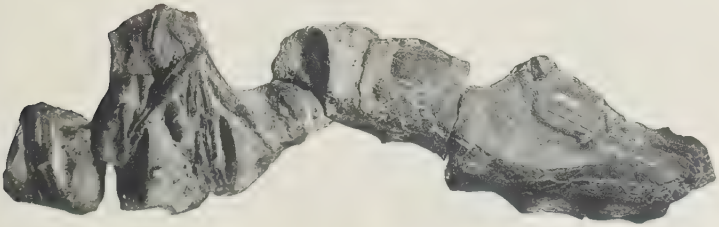
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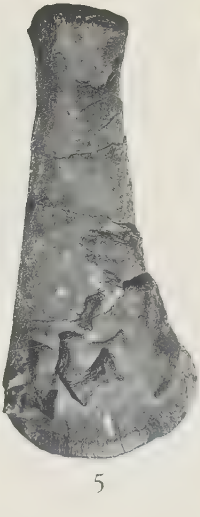
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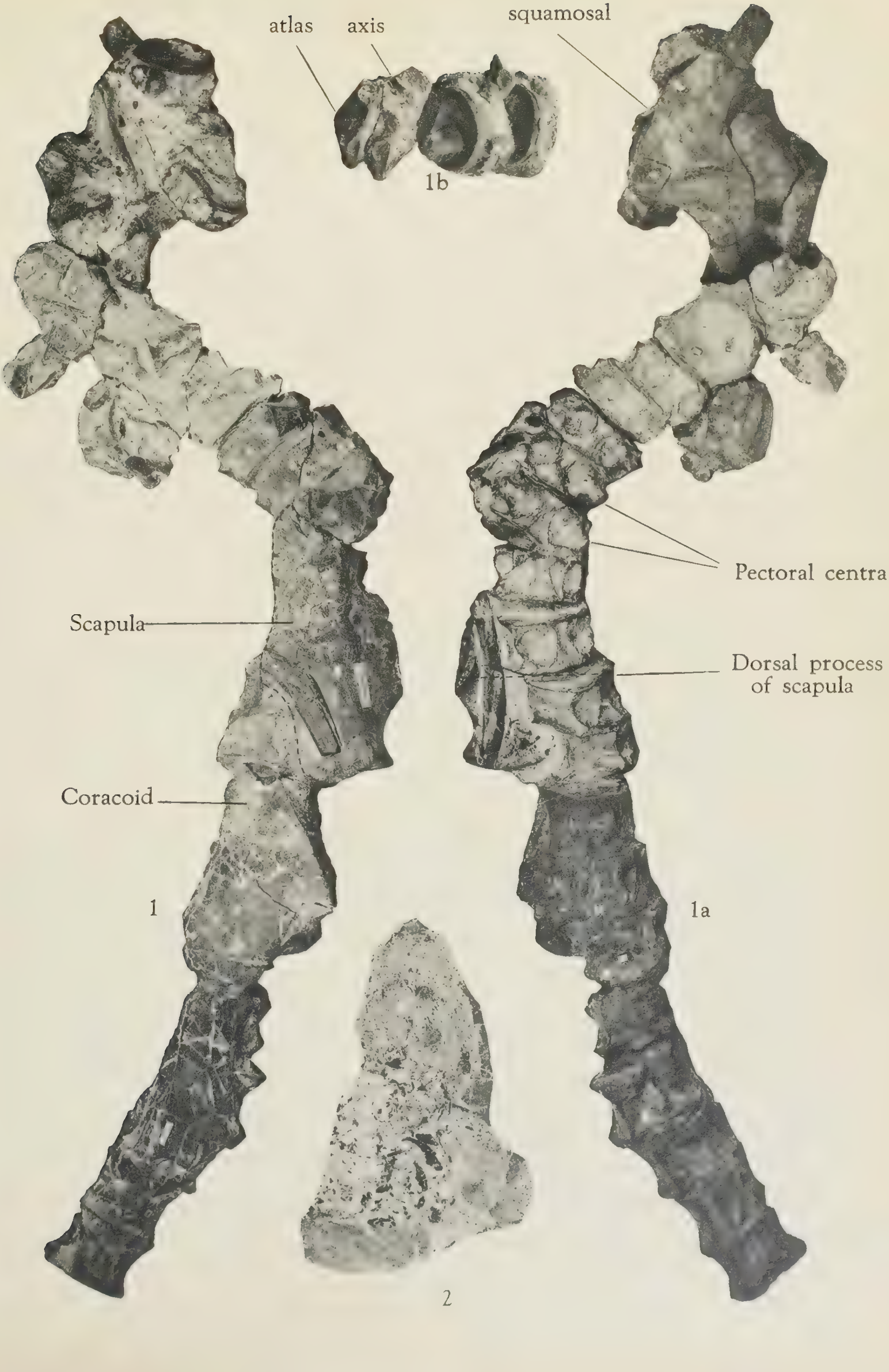

atlas
axis
squamosal
1b
Pectoral centra
Scapula
Dorsal process of scapula
Coracoid
1
1a
2

TARLO, *Pli*

the vertebrae can be used as an indication of their relative position in the body as shown in the table below.

Vertebrae in Block A		*Length (in mm.)*	*Vertebrae in Block A*		*Length (in mm.)*
Anterior Cervical	14th	37	Pectoral	1st	48
	15th	38		2nd	50
Posterior Cervical	1st	40	Dorsal	1st	52
	2nd	42		2nd	56
	3rd	43		7th	67
	4th	44		12th	71

The cervical vertebrae are the most compressed, but these gradually increase in length down the neck. However, in the region of the posterior cervicals and pectoral vertebrae there is a rapid increase, so that by the time the seventh dorsal vertebra is reached its length is almost double that of the anterior cervicals. The vertebrae reach a maximum length in the centre of the dorsal region, and from then on the trend is reversed.

Cervical vertebrae. The first two cervical vertebrae—the atlas and axis—are incomplete, the arch of the atlas and both sub-vertebral wedge bones being missing.

The third vertebra has a pronounced ventral lip directed anteriorly with a marked rugose area behind it on the ventral surface of the centrum, which tends to produce a faint ventral keel. However, in the majority of the cervical vertebrae there is no suggestion of such a ventral keel, and the rugosities on their ventral surface are limited to strips along the anterior and posterior margins.

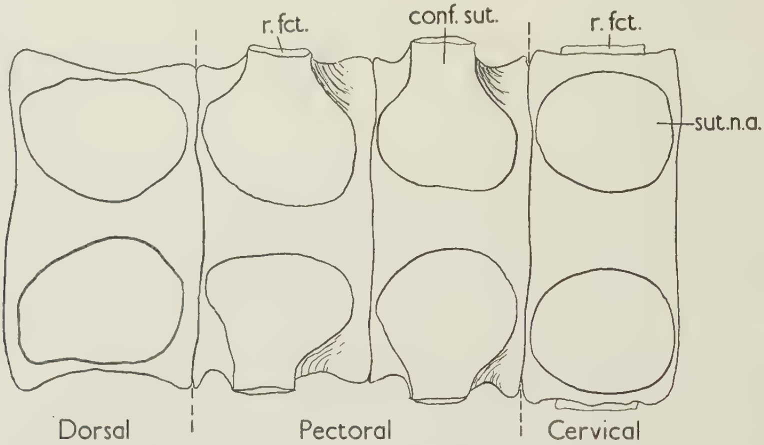
There are double rib facets on the lateral surfaces of the centra of all the anterior cervical vertebrae except the atlas and axis. The inferior facet in each case is more or less circular in outline, while the superior facet tends to be in the form of a triangle, with a narrow ridge extending from its apex to the base of the neural arch.

The articular surfaces of the anterior cervical vertebrae show a well-developed marginal bevel, but this disappears in the posterior cervicals. The articular surfaces are slightly concave and have a small central pit, no mamilla being developed as is the case in other Kimeridgian species.

Posterior cervical vertebrae. In Block A the four most posterior of the cervical centra can be distinguished from the anterior cervical vertebrae by the fact that they have single rib facets, and the bevelling of the margins of the articular surfaces is slight. In view of these differences these four vertebrae are designated posterior cervicals, but this distinction is clearly an arbitrary one, as the neotype itself has a single-rib facet on one side and a double one on the other side.

As in the anterior cervical vertebrae, there are two rugose strips of bone on the ventral surface of the centra—one on the anterior border and one on the posterior. The articular surfaces are slightly concave and each has a depression in the centre, no boss being present such as is found in the posterior cervical centra of other Kimeridgian species. The posterior cervical vertebrae are therefore considered conspecific with the neotype already described, as they possess the two strips of rugose bone on their ventral surface and their articular surfaces show no central convexity and virtually no marginal bevelling.

Pectoral vertebrae. Pectoral vertebrae are defined as those transitional vertebrae in which the articular facet for the rib lies partly on the centrum and partly on the neural arch. This is the intermediate position between cervical vertebrae in which the facet is on the centrum, and dorsal vertebrae where it is on the neural arch. As can be seen from Pl. 52, fig. 1*a* and text-fig. 1, there are only two vertebrae of this type in the Ely specimen, the transition having taken place rapidly.



TEXT-FIG. 1. *Pliosaurus brachyspondylus* (Owen), vertebral centra in dorsal view, showing changes in outline of suture of neural arch as rib articulation rises from body of centrum on to neural arch itself. Sedgk. Mus. J. 35991. × ½. conf. sut., suture of neural arch confluent with rib facet; r.fct., rib facet; sut. n.a., suture of neural arch.

The dorsal view of Block A shows clearly how the suture of the neural arch and the rib facet become confluent during this transition. In these two pectoral centra the lower half only of the rib facet is present on the centrum, the upper half having been borne by the neural arch, which is missing.

Dorsal vertebrae. The rib facet in these vertebrae is borne wholly on the transverse process of the neural arch, and in dorsal view the suture of the neural arch on the centrum reverts to the shape it possessed in the cervical vertebrae, this change in shape being indicated in text-fig. 1.

PECTORAL GIRDLE AND FORELIMB. Sufficient of the left scapula and coracoid are preserved for a full description of them to be given. In addition, a complete right humerus is preserved.

Scapula. The major portion of the left scapula is preserved in one piece on the ventral surface of the second pectoral vertebra and the first four dorsal vertebrae, and can be seen in Pl. 52, fig. 1. The length of the part preserved is 250 mm. and its maximum width is 150 mm.

The ventral surface of the scapula is visible, and it is clear that it is a triradiate bone with a thickened glenoid ramus which bears a facet for the articulation of the coracoid, and another which forms the anterior part of the glenoid cavity. Medially the scapula thins out and is expanded into a broad flat ventral plate, part of which has been broken off. A ridge extends from the glenoid cavity towards the anterior extremity of the scapula, and from this ridge there is a lateral extension of the bone—the dorsal process

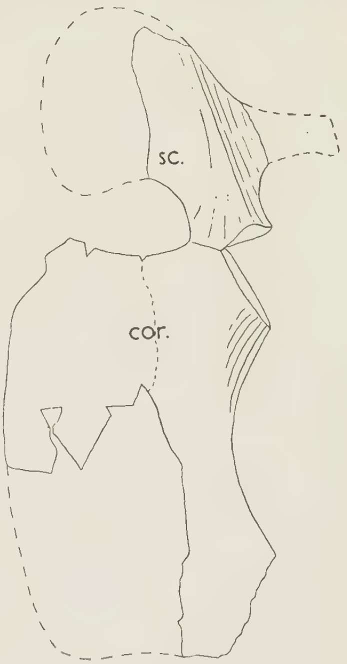
—which is set off at an angle to the plane of the bone. Again part of this process is missing, but in dorsal view the cross-section of the process is clearly visible (Pl. 52, fig. 1*a*).

From the above description and reconstruction in text-fig. 2, it is obvious that the scapula of the Ely skeleton is very similar to that of *Pliosaurus sp.* figured earlier (Tarlo 1958*b*) and is quite different from the scapula of *Pliosaurus macromerus* Phillips.

Coracoid. On the ventral surface of the fifth to the eleventh dorsal vertebrae is preserved the lateral half of the left coracoid, showing both the glenoid and the lateral border. The whole outline including the thickened glenoid portion has suffered no distortion, and although the sheet of bone is fractured it presents a smooth clean edge. The preserved lateral portion of the coracoid is visible in Pl. 52, fig. 1, and as can be seen both from the photograph and from the reconstruction of the pectoral girdle in text-fig. 2 the postero-lateral corner of the bone is somewhat expanded.

Fortunately, in addition a number of fragments of this same bone show the symphysial region of the left coracoid and fit exactly on to the anterior part of the bone which adheres to the vertebral column. It is thus possible to establish the full outline of the coracoid, the measurements of which are: length 500, width 325 mm.

Humerus. This is preserved complete and is indistinguishable from the propodials of most other Pliosaurs. Its rounded head is divided into two sub-equal facets, the dorsal one of which is slightly smaller than the ventral. The bone is dorso-ventrally compressed and expanded distally.



TEXT-FIG. 2. *P. brachyspondylus* (Owen), reconstruction of left side of pectoral girdle in ventral view, Sedgk. Mus. J. 35991. × $\frac{1}{8}$. COR., coracoid; SC., scapula.

PELVIC GIRDLE AND HIND LIMBS. Preserved in a similar way to the pectoral girdle, part of the pelvic girdle is found adhering to the ventral surface of several vertebrae, together with a number of abdominal ribs. In addition, part of an ischium and the complete left femur are known as isolated bones.

Pelvic girdle. Fixed to the ventral surface of the last four dorsal vertebrae of Block B is part of a flat girdle bone measuring 360 mm. in length and having a maximum width of 150 mm. Just anterior to this bone are cemented a number of abdominal ribs, and as the bones seem to be lying more or less as they would in the body, it seems reasonable to assume that the flat girdle bone is part of the pubis (Pl. 51, fig. 4).

In the isolated ischium, the acetabular portion is complete and the greater part of the lateral edge is preserved, but the posterior extremity and medial aspects of this bone are missing. The length of the fragment is 344 mm. and together with the pubis a minimum length of 700 mm. can be established for the pelvic girdle. However, it seems more likely that with the completion of the ischium and also the pubis the full length would be nearer 800 mm.

Femur. The left femur (Pl. 51, fig. 5) is preserved complete, with a number of phalanges adhering to it. This bone is very similar to the humerus in its proportions although it is larger, as can be seen from the comparative table below, the measurements being given in mm.

	Humerus		*Femur*	
	width	*thickness*	*width*	*thickness*
Head	89	90	105	96
Half-way down shaft	104	55	112	61
Distal end	180	52	200	57
Total length	400		450	

DISCUSSION

The significance of the Ely skeleton is that it provides the means whereby the Kimeridgian Pliosaurs can be separated into two groups each with a distinct type of mandible and scapula. *Pliosaurus brachydeirus* and *P. brachyspondylus* belong to one group which has a mandible in which there is a long symphysis containing ten to twelve teeth of which the anterior five to six are large and caniniform, and a scapula in which the dorsal process is set off at an angle to the rest of the bone and is produced laterally or posterolaterally. The second group, represented by *P. macromerus*, is characterized by a mandible with a short symphysis bearing only five to six large caniniform teeth, and a scapula in which the dorsal process is in the same plane as the rest of the bone, and is produced anteriorly.

The differences between the two groups are such that it is no longer feasible to retain them both in the genus *Pliosaurus*, which name must be kept for the group containing the type species, *P. brachydeirus*. In a later paper I shall propose a new generic name for *P. macromerus*.

Acknowledgements. I wish to thank Professor D. M. S. Watson for very helpful criticism of the manuscript, Dr. P. L. Robinson for valuable discussions, and Dr. W. E. Swinton for unfailing help and advice. I am grateful to Mr. A. G. Brighton and Dr. C. L. Forbes of the Sedgwick Museum, Cambridge, for assistance and loan of specimens. Pl. 51, figs. 1, 1*a–c*, 3, 3*a* and Pl. 52, fig. 2 were photographed by Mr. A. Veenstra; all other photography by Mr. A. Barlow. My thanks are also due to D.S.I.R. since the work embodied in this paper was carried out during the tenure of a Research Studentship.

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FOUR BRITISH ORDOVICIAN SPECIES OF DALMANELLOID BRACHIOPOD

by R. CAVE AND W. T. DEAN

ABSTRACT. Lectotypes are chosen for certain Caradoc brachiopod species of zonal value, and their stratigraphical horizons and associated faunas are reviewed. *Paucicrura sowerbii* nom. nov. is proposed for the Ordovician syntype of *Orthis canalis* J. de C. Sowerby, 1839.

A NUMBER of brachiopods of Caradoc age have hitherto been described in detail, but with each species represented only by a collection of syntypes from differing localities. In view of the modern refinements of Caradoc stratigraphy, and the growing stratigraphical importance of many brachiopods, it is considered advisable that definition of some of these species should be more precise. The writers are indebted to Mr. R. G. Coope (University of Birmingham) and Mr. J. D. D. Smith (Geological Survey and Museum) for the loan of type material. W. T. Dean publishes this paper by permission of the Trustees, British Museum (Natural History).

Family DALMANELLIDAE Schuchert and Le Vene 1929
= Wattsellidae Schuchert and Cooper 1931

Genus DALMANELLA Hall and Clarke 1892

1928 *Wattsella* Bancroft, p. 55.

Type species. Orthis testudinaria Dalman 1828 by original designation of Hall and Clarke (1892, p. 205).

In 1928 Brancroft (p. 55) erected the genus *Wattsella*, selecting *Wattsella wattsi* Bancroft as the type species. The following year four new species of the genus were introduced, namely *Wattsella sp. A*, *W. sp. B*, *W. sp. C*, and *W. sp. D* (Bancroft 1929*a*, pp. 36–38; 1929*b*, table facing p. 76), but although used in a zonal classification of Caradoc strata as characteristic forms within the Lower Longvillian substage, they were left undescribed. Later, in a private publication, Bancroft (1933, table 2) again mentioned these species, giving them the new names *Wattsella horderleyensis*, *W. lepta*, *W. indica*, and *Raymondella typa* respectively. The new generic name *Raymondella* was given only a brief diagnosis (Bancroft 1933, p. 3) and the undescribed *R. typa* was chosen as type species. Under Article 25 (3) of the International Rules of Nomenclature all these names were invalid, and remained so until 1938 when three of them, *W. horderleyensis*, *W. indica*, and *R. typa* were described and figured. The author of the descriptions, and thus of the species, was Whittington (1938*a*, pp. 50–51; 1938*b*, pp. 245–7), though he retained Bancroft's manuscript names. In a later paper Bancroft gave his first account of the same three species (1945, pp. 190–95, 198–201) and claimed them as new, apparently not recognizing Whittington's authorship and basing his descriptions solely on Shropshire specimens now in the British Museum (Natural History). Whittington's descriptions

Palaeontology, Vol. 1, Part 4, 1959, pp. 292–7, pl. 53.]

made in 1938 did not select holotypes, but were formulated on syntypes numbering up to four for each species. In every case, however, the figured syntypes included North Welsh specimens together with at least one specimen from those places in south Shropshire which were intended by Bancroft (*in litt.* to H. B. Whittington) to be the type-localities (Whittington 1938*a*, p. 51; 1938*b*, pp. 247, 250. See also Bancroft 1945, pp. 193, 195, 201). It now appears desirable to select lectotypes of the above species, and in every case we have thought fit to choose the syntype utilized by Whittington from the south Shropshire locality advocated by Bancroft, though there appears no doubt as to the specific identity of the Shropshire and Welsh specimens.

Dalmanella horderleyensis (Whittington *ex* Bancroft MS.)

Plate 53, fig. 1

1839 *Orthis testudinaria* Dalman, J. de C. Sowerby *in* Murchison, p. 640, pl. 20, figs. 9, 10.
1854 *Orthis testudinaria* Dalman, J. de C. Sowerby *in* Murchison, pl. 6, figs. 1, 2.
1859 *Orthis testudinaria* Dalman, J. de C. Sowerby *in* Murchison, pl. 5, figs. 1, 2.
1929*a* *Wattsella sp. A.* Bancroft, pp. 36, 37.
1929*b* *Wattsella sp. A.* Bancroft, table facing p. 76.
1933 *Wattsella horderleyensis* Bancroft, table 3. MS. name only.
1938*a* *Wattsella horderleyensis* Bancroft, Whittington, p. 50, pl. 6, figs. 2–7.
1945 *Wattsella horderleyensis* n.sp., Bancroft, p. 190, pl. 22, figs. 1–3, pl. 23, figs. 1–3, pl. 24, fig. 1.
1958 *Dalmanella horderleyensis* (Whittington), Dean, p. 206, pl. 24, figs. 12, 13.

Lectotype (here selected). Geol. Dept. Mus., University of Birmingham, T. 218, internal mould of a dorsal valve from Long Lane Quarry, two-thirds of a mile south-west of Cheney Longville, Shropshire.

Paratypes. T. 217, internal mould of a ventral valve, locality as for lectotype. T. 219 and T. 222, internal moulds of ventral and dorsal valves respectively, from Lluest Quarry, Allt-y-Gader, Llanfyllin, Montgomeryshire. T. 220 and T. 221, internal moulds of ventral and dorsal valves respectively, from trench-like quarry 200 yards east of Bwlch-y-Cibau Church, Montgomeryshire. All specimens are in the Geol. Dept. Mus., University of Birmingham.

Dalmanella indica Whittington *ex* Bancroft MS.

Plate 53, figs. 2–4

1929*a* *Wattsella sp. C.* Bancroft, p. 37.
1929*b* *Wattsella sp. C.* Bancroft, table facing p. 76.
1933 *Wattsella indica*, Bancroft, table 2. MS. name only.
1938*b* *Dalmanella* (*Wattsella*) *indica* (Bancroft), Whittington, p. 245, pl. 10, figs. 4–7.
1945 *Wattsella indica* n.sp., Bancroft, p. 194, pl. 22, figs. 8–12; pl. 23, figs. 5, 6.
1958 *Dalmanella indica* Whittington, Dean, p. 206, pl. 24, fig. 14.

Lectotype (here selected). No. 234 (= 299), Geol. Dept. Mus., University of Birmingham, internal mould of dorsal valve from quarry by west side of track near north-east side of Longville Plantation, 2 miles west-north-west of Cheney Longville, Shropshire. In a personal communication Professor H. B. Whittington has confirmed that in his original description (1938*b*, explanation of pl. 10) ‘north-east side’ was misprinted as ‘north-west side’.

Paratypes. No. 233 (= 298), internal mould of dorsal valve from the old quarry 1 mile east of point 822 in Ancient Camp, Bryngwyn Hill, 3 miles east-south-east of Llanfyllin, Montgomeryshire. Nos. 235 (= 300) and 236 (= 301), internal moulds of dorsal and ventral valves respectively, from mudstones between ash and conglomerate, quarry at Bryn Farm, 1 mile south-east of Glyn Ceiriog, Denbighshire. All specimens in the Geol. Dept. Mus., University of Birmingham.

Discussion. Considerable variation is noted in the shape and size of the cardinal process in individuals from the same horizon and locality (see Pl. 53, figs. 3, 4).

Genus BANCROFTINA Sinclair 1946

1933 *Raymondella*, Bancroft, p. 3. MS. name only.
1938*b* *Raymondella*, Whittington, p. 249. Non *Raymondella* Reed 1935.
1945 *Raymondella*, Bancroft, p. 197.

Type species. Raymondella typa Whittington 1938 by original designation of Sinclair (1946, p. 295).

Bancroftina typa (Whittington *ex* Bancroft MS.)

Plate 53, figs. 5, 6

1929*a* *Wattsella sp. D.*, Bancroft, p. 38.
1929*b* *Wattsella sp. D.*, Bancroft, table facing p. 76.
1933 *Raymondella typa*, Bancroft, table 2. MS. name only.
1938*b* *Raymondella typa* Bancroft, Whittington, p. 249, pl. 10, figs. 12–14.
1946 *Bancroftina typa* (Bancroft), Sinclair, p. 295.
1949 *Bancroftina typa* (Whittington), Sinclair, p. 438.
1958 *Bancroftina typa* (Whittington), Dean, p. 206, pl. 24, figs. 17, 18.

EXPLANATION OF PLATE 53

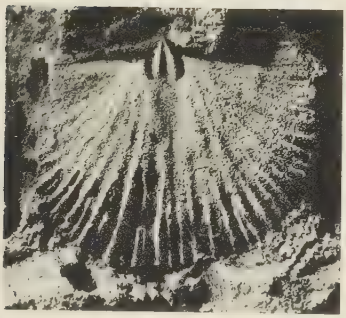
Fig. 1. *Dalmanella horderleyensis* (Whittington). Lower Longvillian substage, Long Lane Quarry, ⅔ mile south-west of Cheney Longville, Shropshire. Lectotype, Birmingham University T. 218, internal mould of dorsal valve, ×2·8.

Figs. 2–4. *Dalmanella indica* Whittington. Lower Longvillian substage, old quarry by west side of track near north-east side of Longville Plantation, ½ mile north-west of Cheney Longville, Shropshire. 2, B.M. BB. 24889, latex impression of dorsal valve, ×3. 3, lectotype, Birmingham University 234, internal mould of dorsal valve, ×2·5. 4, B.M. BB. 24888, internal mould of dorsal valve showing another form of cardinal process, ×2·7.

Figs. 5, 6. *Bancroftina typa* (Whittington). Lower Longvillian substage, old quarry by west side of New House, Horderley, Shropshire. 5, lectotype, Birmingham University 242, internal mould of dorsal valve, ×2·5. 6, B.M. BB. 24892, latex impression of dorsal valve, ×2·8.

Figs. 7–11. *Paucicrura sowerbii* nom. nov. Lower Longvillian substage, all specimens figured here are from the *Dalmanella horderleyensis* zone. 7, holotype, G.S.M. Geol. Soc. Coll. 6852, internal mould of dorsal valve, ×3·1. 8, paratype, B.M. BB. 24885, internal mould of dorsal valve, ×3·1. 9, 11, paratype, B.M. BB. 24886, internal mould of ventral valve showing pallial sinuses, ×3·1. 10, B.M. BB. 24891, internal moulds of two ventral valves showing different development of pallial sinuses, ×3·1. Fig. 7 is localized merely as ‘Myfod’. 8, 9, and 11 are from the large exposure on Gallt-yr-Ancr, 440 yards west-north-west of Dyffryn, ½ mile south-west of Meifod, Montgomeryshire. 10 is from Long Lane Quarry, ⅔ mile south-west of Cheney Longville, Shropshire.

Photographs by W. T. Dean.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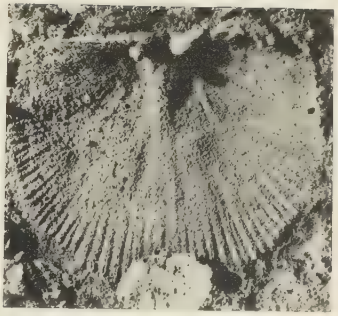
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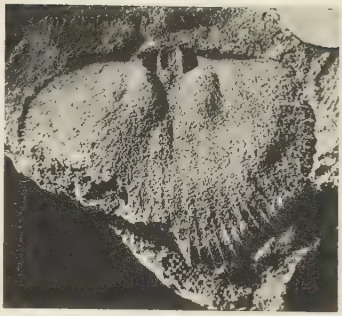
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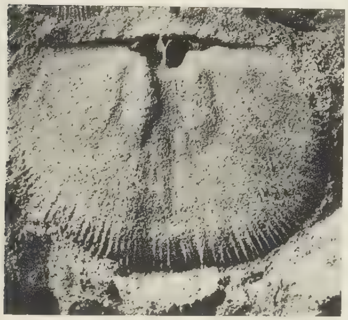
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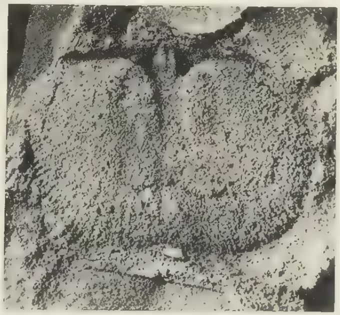
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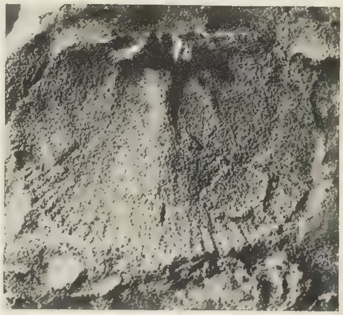
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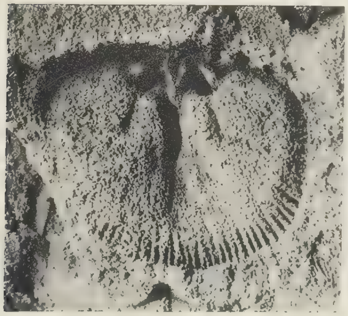
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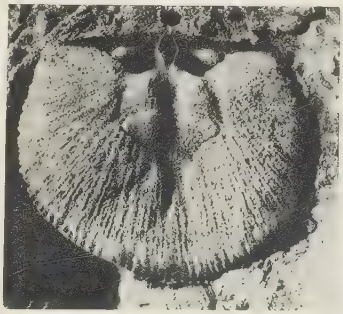
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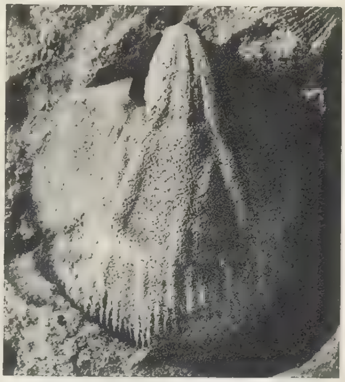
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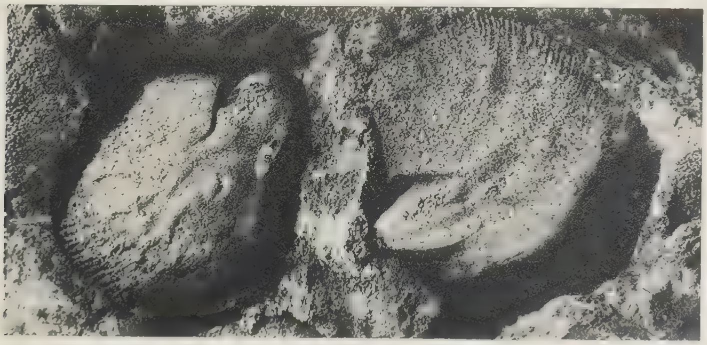
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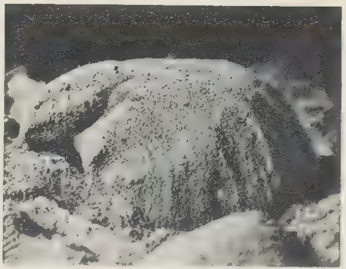
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CAVE and DEAN, Ordovician Dalmanellids

Lectotype (here selected). No. 242 (= 307), Geol. Dept. Mus., University of Birmingham, internal mould of dorsal valve from quarry at New House, $\frac{2}{3}$ mile north-west of Cheney Longville, Shropshire.

Paratypes. No. 241 (= 306), internal mould of ventral valve from crag 330 feet south-east of Pen-y-Graig Farm, 1 mile south of Glyn Ceiriog, Denbighshire. No. 243 (= 308), internal mould of dorsal valve, loose block from outcrop 400 feet north-west of Bryn Farm, 1 mile south-east of Glyn Ceiriog. Both specimens in the Geol. Dept. Mus., University of Birmingham.

Genus PAUCICRURA Cooper 1956.

Type species. Orthis rogata Sardeson 1892 by original designation.

When Bancroft erected the genus *Resserella* (1928, p. 54) he cited as type species *Orthis canalis* J. de C. Sowerby. The latter was described by Sowerby (*in* Murchison 1839, p. 630, pl. 13, fig. 12*a*, p. 640, pl. 20, fig. 8) using syntypes from two different horizons. One of these syntypes, G.S.M. Geol. Soc. Coll. 51550 (Murchison 1839, pl. 13, fig. 12*a*) was obtained from the Wenlock Shales, and figured together with numerous other Wenlock Shale fossils, though the species was said to occur also in the Caradoc Sandstone. Localities given were 'Delves Green; Croft; Tame Bridge; Woolhope (Falfield, near Tortworth)'. The rest of Sowerby's figured syntypes, G.S.M. Geol. Soc. Coll. 6852 (*in* Murchison 1839, pl. 20, fig. 8), originated at Meifod, though the species was described as occurring 'in Caradoc Sandstone at Horderley and Whittingslow, near the Caradoc; Moel-y-garth and Gaerfawr, near Welchpool', and 'in Llandeilo Flags at Clog-y-frain; Golden Grove, Caermarthenshire; at Llampeter-felfrey, Pembrokeshire'. Sowerby claimed that the interiors of the species were figured 'to show how they differ from the allied species in the higher beds of the Upper Silurian rocks. The specimens are larger than those in the Wenlock Shale.'

Schuchert and Cooper (1932, p. 126) designated Sowerby's specimen from the Wenlock Shales as lectotype, with unfortunate consequences. Stubblefield has pointed out (*in* Cooper 1956, p. 956) that the specimen involved is a typical *Parmorthis* Schuchert and Cooper (1931, p. 246), so making this genus a subjective synonym of *Resserella* Bancroft 1928. In the meantime the name *Resserella canalis* had been frequently applied to Caradoc brachiopods which constitute a well-known and stratigraphically useful species in the Lower Longvillian substage of south Shropshire and North Wales. As Sowerby's syntypes are generically dissimilar, and as *Resserella* must be used for Silurian shells hitherto known as *Parmorthis*, Cooper has erected a new name *Paucicrura* to include the Ordovician brachiopods previously called *Resserella*, using as type species *Orthis rogata* Sardeson 1892, a form which has been referred also to *Onniella* Bancroft 1928 (Whittington 1938*b*, p. 245). The outcome of this situation is that one of Sowerby's syntypes is now called *Resserella canalis*, whilst the other syntype, representing what many Ordovician stratigraphers have in the past called *R. canalis*, is generically referable to *Paucicrura* but is in need of a new specific name, for which *P. sowerbii* is now proposed.

Paucicrura sowerbii nom. nov.

Plate 53, figs. 7–11

1839 *Orthis canalis* J. C. de Sowerby *in* Murchison, p. 640, pl. 20, fig. 8.

1854 *Orthis elegantula* (*canalis*) Dalman, J. de C. Sowerby *in* Murchison, pl. 6, fig. 5.
1859 *Orthis elegantula* Dalman, J. de C. Sowerby *in* Murchison, pl. 5, fig. 5.
1928 *Resserella canalis* (Sow.), Bancroft, p. 54.
1929 *Resserella canalis* Sowerby, Bancroft, pp. 36–38.
1932 *Resserella canalis* (Sowerby), Schuchert and Cooper, p. 126, pl. 17, figs. 14–16.
1938*a* *Resserella canalis* (J. de C. Sowerby), Whittington, p. 51, pl. 6, figs. 8–12.
1945 *Resserella canalis* Sowerby, Bancroft, pp. 193, 195, 203.
1958 *Resserella canalis* (J. de C. Sowerby), Dean, p. 221.

Diagnosis. The species has already been described in detail by Whittington (1938*a*, p. 51) and little further need be added. It is noted, however, that the ridge bounding the dorsal muscle impressions is subject to variation and is very strongly developed in some specimens (Pl. 53, fig. 8). In addition the vascular impressions of the ventral valve show variable development according to the size of the individual; the larger the specimen the more prominent the feature is likely to be.

Holotype. G.S.M. Geol. Soc. Coll. 6852 (Pl. 53, fig. 7). *Paratypes.* Brit. Mus. (Nat. Hist.) BB. 24885 (Pl. 53, fig. 8), BB. 24886 (Pl. 53, figs. 9, 11).

Locality and horizon. The holotype is the dorsal valve figured by Sowerby (*in* Murchison, 1839, pl. 20, fig. 8), and forms part of a block of weathered sandy limestone filled with the remains of brachiopods. The ventral valve figured by Sowerby (loc. cit.) and shown by him as being on the same block has not been traced with certainty, and his drawing is obviously composite. The specimen is labelled 'Myfod' only, and the associated fauna includes *Dalmanella horderleyensis* with occasional *Broeggerolithus* and *Phacopidina*. In view of the lack of adequately-preserved material on the original hand-specimen, paratypes have been chosen from well-localized Meifod specimens in the British Museum (Natural History), and these derive from the large exposure on Gallt-yr-Ancr, 440 yards just north of west from Dyffryn, ½ mile south-west of Meifod Church. At this locality *Paucicrura sowerbii* occurs with *Dalmanella horderleyensis* and *Broeggerolithus*, and the rocks belong to the Lower Longvillian substage. The other specimens figured (Pl. 53, fig. 10) come from the Lower Longvillian (Middle Horderley Sandstone *pars*) of Long Lane Quarry, two-thirds of a mile south-west of Cheney Longville, Shropshire, where the associated fauna is for the most part similar to that at Meifod.

DISTRIBUTION

In the type-area of the Caradoc Series in south Shropshire the appearance of *Dalmanella horderleyensis* in large numbers marks the base of the Lower Longvillian substage, and, so far as is known, this line of demarcation holds good for the whole of North Wales. In Denbighshire and Montgomeryshire the species is accompanied by the more typically Soudleyan brachiopod *Rafinesquina expansa* (J. de C. Sowerby), and such an overlap may be characteristic in all parts of North Wales, though these two species have not yet been found co-existing in south Shropshire. In the Meifod and Welshpool districts of Montgomeryshire *D. horderleyensis* appears with large numbers of *Paucicrura sowerbii*, a species which continues beyond the range of *D. horderleyensis* to the end of the succeeding *Dalmanella indica* and *D. lepta* zone, where the specimens are fewer but slightly larger. Bancroft distinguished separate zones characterized by

D. indica and *D. lepta* (Bancroft), but it has been found preferable, both in south Shropshire and at Welshpool, to combine the two as a single zone within the Lower Longvillian, although *D. lepta* has not yet been found in the Welshpool district. At Welshpool *Nicolella actoniae* (J. de C. Sowerby), *Platylichas* and *Chasmops* appear below the top of the zone of *Dalmanella indica* and *D. lepta*, and the first two continue into the succeeding *Bancroftina typa* zone. In south Shropshire *Chasmops* has not been found earlier than the Upper Longvillian, and a single record of *Platylichas* from the *B. typa* zone of the Onny Valley has not yet been substantiated.

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ARENACEOUS FORAMINIFERA FROM THE TYPE KIMERIDGIAN (UPPER JURASSIC)

by ADRIAN J. LLOYD

ABSTRACT. A series of 105 samples with an average vertical spacing of 12 ft. was collected to span the Kimeridge Clay of the Dorset Coast. The dominant element of the foraminiferal faunas comprised members of the family Lagenidae; agglutinating forms were an important accessory.

The proportions of potentially agglutinable materials in each of twenty-seven samples were determined. A study was also made of the materials used by the 'arenaceous' foraminifera in building their tests. The two sets of results indicate that species agglutinate a preferred grain-size and, in some cases, a preferred type of material. This agrees broadly with Hofker's (1953) conclusions.

Systematic descriptions are given of twenty-five species of arenaceous foraminifera, referred to eight genera. Three species are new.

INTRODUCTION

BY contrast with the foraminifera of the rest of the Jurassic those in the uppermost part have received scant attention. In his account of the Kimeridge Clay of England, Blake (1875) gave only a list of foraminifera. Woodward (1895, pp. 399–401) gives lists of foraminifera, and a shorter list of forms from the Hartwell Clay was given by Chapman (1897). The latter were described by Neaverson (1921), but only a brief note is made of many species. Finally, Waterston (1951) included a list of genera found in the Kimeridgian of Eathie, Cromarty, Scotland.

On the European continent the foraminifera are known in more detail. Alth (1882) described the foraminifera of the Nisniow Limestone, later redescribed by Cushman and Glazevski (1949). The most comprehensive account of the Polish forms is by Bielecka and Pożaryski (1954), but the important work on Russian foraminifera by Myatliuk (1939) has not been seen. Of lesser importance are papers by Chapman (1900), Tobler (1928), Mohler (1938), and Klingler (1955).

It was thought best to begin an investigation of the British Kimeridgian foraminifera from the rocks exposed along the Dorset Coast between Weymouth and Swanage, as here the whole formation is exposed and Arkell (1947, pp. 64–88) has provided a detailed account of the sections. Moreover, d'Orbigny selected this as the type-area of the Kimeridgian Stage. The subdivision of the Kimeridge Clay (the exact equivalent of the Kimeridgian Stage) given by Arkell (1947) is adopted here. Some members of the Kimeridge Clay have been given names, e.g. Crushed Ammonoid Shales, see text-fig. 1. Attention was concentrated on two areas, first, the gentle southern limb of the Purbeck anticline from Kimeridge Bay to Hounstout, where samples from the middle of the *pseudomutabilis* zone to the top of the formation were obtained, and second, the cliffs between Shortlake and Osmington Mills (the Black Head sections), where the *baylei*, *cymodoce*, *mutabilis* zones and the lower part of the *pseudomutabilis* zone were sampled. From this composite section of some 1,200 ft. of strata, 105 samples were collected. Each sample was given a code number of three elements representing locality (e.g. 'Do-' for Dorset Coast), ammonite zone (e.g. 'Mu' for *Rasenia mutabilis*), and position in the zone (samples numbered from oldest to youngest).

[Palaeontology, Vol. 1, Part 4, 1959, pp. 298–320, pl. 54.]

Standard preparation methods were employed. All specimens were picked from most residues and further more rapid methods showed that the other samples yielded a representative fauna. The material picked from each sample was sorted initially into ‘form-groups’ (species, species-groups, or closely allied species). A few specimens from each form-group, selected to show the range of variation within that group, were mounted for further study. Thus the variation of each species both at a given horizon and in time could be determined. This led to a broad interpretation of the species, some of which can be subdivided. Two or more of these sub-specific groups of a single species may occur in the same sample so cannot be regarded as sub-species or varieties. They are taken here as lying outside the scope of the International Rules and will be distinguished by capital letters (e.g. *A. agglutinans* A, *A. agglutinans* B, &c.).

Only the Jurassic literature, and in some cases Ellis and Messina’s Catalogue, were consulted in compiling the synonymies which should therefore be taken only as lists of morphologically similar forms. Type and figured specimens have been deposited in the British Museum (Natural History).

The author is indebted to Dr. Tom Barnard of University College, London, for advice and for reading the manuscript; to Miss S. Jackson for preparing the photographs, and to the Department of Scientific and Industrial Research for a Maintenance Grant.

NATURE OF THE RESIDUES

The Kimeridgian of the type locality is represented by an argillaceous formation, the Kimeridge Clay. At first sight only two lithologies seem to occur—shales, with the laminations well or poorly developed, and cementstone bands, thin compact limestones. As the treatment of limestones involves special techniques they have not been considered here. A closer inspection of the ‘shales’ shows that many rock-types can be found, ranging from soft, black clays and shaly clays through hard, calcareous clays (Arkell’s ‘Dicey clays’) and soft shales to hard, splintery shales and even sulphurous paper shales. In addition nearly all the beds contain arenaceous material which, in some cases is sufficiently common to be visible macroscopically (the ‘Marls’ of stratigraphers). The distribution of these rock-types in the vertical sequence is broadly cyclical (text-fig. 1). The soft clays and shales predominate in the lower and upper parts of the formation while the hard shales are found mainly in the middle. The sandy clays are found only at the extreme base and towards the top.

The lithological characters may be summarized as follows:

1. The *baylei* zone. Sandy clay.
2. The two *Rasenia* zones. Soft, gypsiferous clays becoming shaly near the top.
3. The *pseudomutabilis* and two *Gravesia* zones. Hard, often paper shales.
4. The *Subplanites* and *pectinatus* zones. Alternations of hard shales and dicey clays or soft shales, the clays becoming dominant upwards.
5. The two *Pavlovia* zones. Soft shales and clays below, becoming sandy clays upwards.

Thin compact limestones occur in 3 and 4. Their names and horizons are indicated in text-fig. 1.

Although agglutinating foraminifera occur throughout the formation only a few species range from bottom to top. Twenty-seven samples were selected for detailed study and their residues analysed. In the following paragraphs a comparison will be made of the materials available, as shown by these samples, and the materials agglutinated.

When the samples were prepared the sole object was to separate foraminifera, of 200 μ diameter or over, from the much finer-grained clay minerals. As a result much material of grain size less than 20 μ has been washed away, including in the upper size range, potentially agglutinable material. A partial check on this lost material can be made from incompletely broken down pieces of shale or marl, from which it seems the loss is slight.

The residues contained eight different classes of material which have been considered as available for agglutination. Gypsum crystals were abundant in residues from the lowest three zones, and less regularly in the *rotunda* zone. This has been ignored as being a secondary constituent.

Quartz. Occurred in every residue with the exception of Do-Pa 8. The usual varieties were clear and yellow-tinted grains, but grey, white, pink, green, and brown-tinted grains also occurred. Included here are two much rarer types, a red garnet and minute lydite pebbles.

Shell fragments. Broken pieces of lamellibranch, gastropod, and ammonite shell were always present, and in many cases formed the bulk of the residue. I think that the presence of patches of pyrite covering broken edges shows that at least some fragmentation was contemporaneous with sedimentation and did not happen during the preparation of the samples.

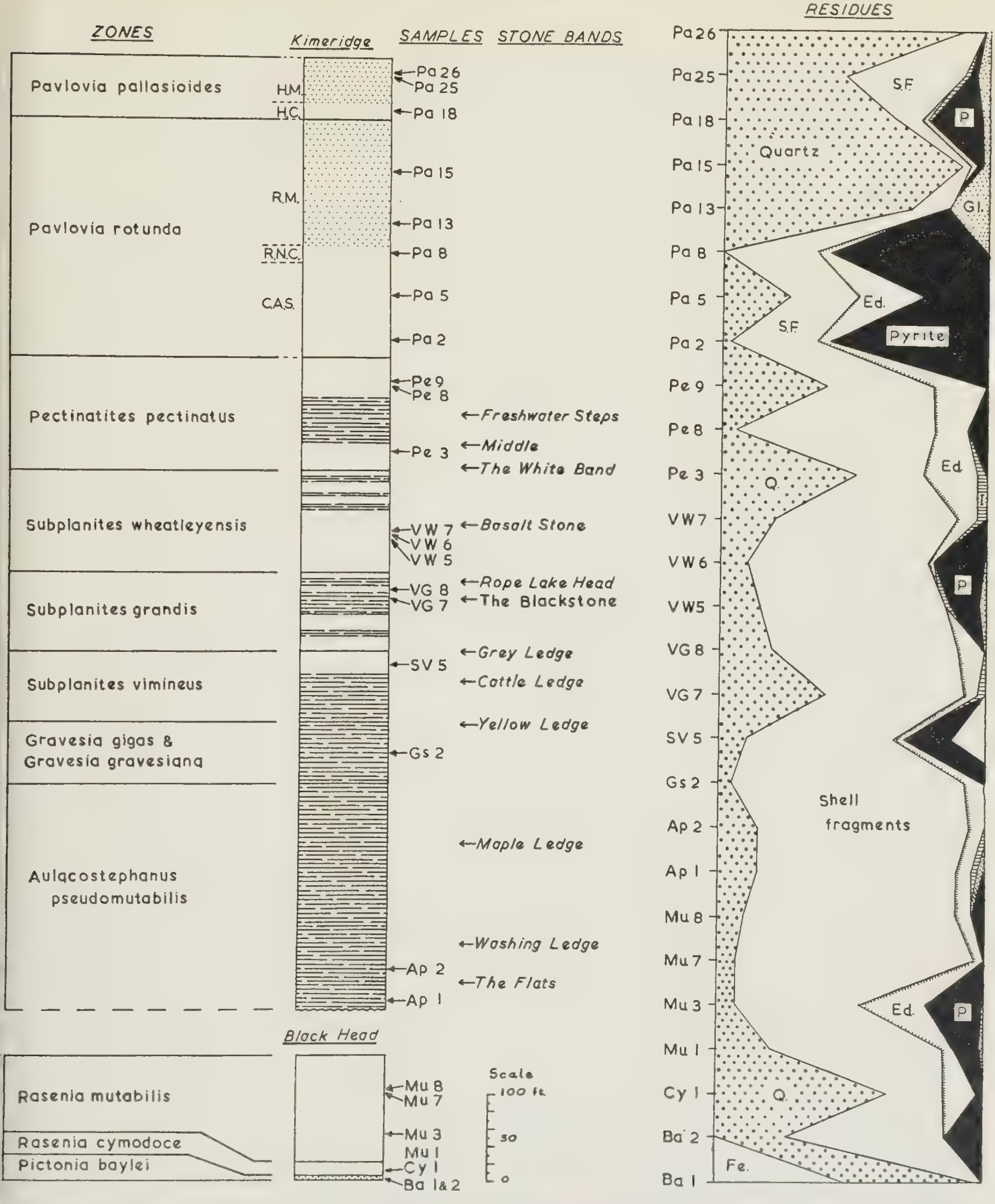
Echinoderm remains, &c. Under this heading are grouped unbroken but disarticulated units. Echinoid plates, spines, and dactylous pedicellariae occurred frequently. Crinoid ossicles of the *Pentacrinus* type and Holothurian spicules were rare, but Ophiuroid ossicles were sometimes common. Also included are fish teeth, fin radials, scales and vertebrae, and Lepadomorph barnacle plates.

'*Inoceramus*' *prisms.* These were never an important element of the residues. All prisms from thick-shelled Lamellibranchs were included here regardless of whether they were derived from *Inoceramus* or not.

Pyrite occurred as sticks and pellets with either a fine-grained, smooth surface or a mammilate surface. With these were found minute globules, the same size as the mammilae of the larger pellets which might therefore be aggregate masses, and perfect crystal cubes. The grain size of these latter types usually falls within the 5–15 μ range. In addition to these 'independent' types, pyrite was also found filling pores in, replacing, or forming a skin on shell material, wood, &c. Love (1957) has shown that the small globules have an organic origin and were penecontemporaneous with sedimentation. I had independently come to the conclusion that at least some of the pyrite was available on the sea floor for agglutination.

Iron pellets. In the *baylei* zone of the Black Head area the lateral equivalent of the Abbotsbury Iron Ore is, in part, a sandy clay with some of the characteristic pellets still occurring. This material, due probably to its large grain size and unwieldy shape, was never agglutinated.

Iron flakes. This constituent occurred in a few samples as irregular, rusty plates. In one sample from the *vimineus* sub-zone, it made up 15 per cent. of the residue. It was never agglutinated.



TEXT-FIG. 1. Zonal classification, lithologies, and available materials of the Dorset Coast Kimeridgian. Left-hand column: zonal scheme after Arkell (1956). Key to lithologies: stippled—sandy clay; shaded —hard shales; blank—soft shales and clays. R.N.C.—*Rotunda* Nodule Clays; R.M.—*Rhynchonella* Marls; H.C.—Hounstout Clay; H.M.—Hounstout Marls; C.A.S.—Crushed Ammonoid Shales. Horizons of the twenty-seven selected samples are indicated. Right-hand column: proportional occurrences of potentially agglutinable materials: Fe.—iron pellets; coarse stipple Q.—quartz; S.F.—shell fragments; shaded edge Ed.—echinoderm fragments, &c.; black P.—pyrite; shaded I—'*Inoceramus*' prisms; fine stipple Gl.—glauconite; blank near right-hand edge—iron flakes.

Glauconite. This is usually a rare element of the residues and is agglutinated along with garnet as a 'quartz substitute'.

The proportional occurrences of these eight elements are shown in the right-hand column of text-fig. 1. No attempt has been made to give absolute quantities as the object is to show the relative availability of any potentially agglutinable material at a given horizon.

It can be seen that quartz is usually present, making up a large proportion of the residue in the *baylei* zone and the top of the *Pavlovia* zones. At these horizons the quartz is also of a coarser grain. Although shell fragments form the bulk of the residues through much of the column, and made up 47 per cent. of the residue from Do-Mu 3, this was the only time they were extensively utilized for agglutination. Pyrite was observed throughout the Kimeridgian so availability alone would not account for its utilization in the middle and upper parts of the succession. The other constituents made up only a minor part of the residues.

UTILIZATION OF THE AVAILABLE MATERIALS

In investigating the utilization of materials two approaches each yield useful information. The first is to observe the differences in materials agglutinated by the same species from different samples; the long-range forms are of special interest here: and the second, to compare the materials used by different species from the same sample.

The grain sizes of agglutinated materials are for convenience divided into three classes, 5–20 μ material called fine grained, 20–60 μ medium grained, with a sub-division into fine-medium and coarse-medium, and over 60 μ coarse grained.

(*a*) Variation in the long-range forms. *Proteonina difflugiformis* (Brady) shows a preference for medium-grained quartz, but variation does occur in both the grain size and type of material. In the *baylei*, *cymodoce*, and *mutabilis* zones clear quartz with grain sizes between 40 and 60 μ was usually agglutinated. Occasionally individuals include finer material and in some samples the maximum grain size was only 30 μ. In some forms pyrite and garnet were included to a small extent. In sample Do-Mu 3 up to 10 per cent. of the material was broken shell of a similar grain size to the quartz. From the *pseudomutabilis* zone to the lower part of the *rotunda* zone the dominant material was finer grain quartz, but from the *wheatleyensis* sub-zone onwards up to 40 per cent. 5 μ pyrite was included. Above the Crushed Ammonoid Shales there was a gradual return to medium-grained quartz, with a corresponding diminution in the amount of pyrite.

Ammobaculites agglutinans (d'Orbigny) has a similar history. In the lower zones fine-medium quartz was the usual material with shell fragments as a minor constituent in Do-Mu 3. In the middle of the Kimeridgian there was a slight reduction in grain size to 10–20 μ, and in a variant with a slender test much 5 μ pyrite was included. In the *pectinatus* zone the normal forms began to include a small amount of pyrite but towards the top of the *Pavlovia* zones there was a return to the fine-medium grain quartz. This species is clearly more conservative than *P. difflugiformis* but appears to follow the same trend.

Ammobaculites deceptorius (Haeusler) always agglutinated finer-grained material, 20–30 μ quartz in the *baylei* zone, and in the *mutabilis* zone utilized more pyrite than any of the above forms. By the *wheatleyensis* sub-zone a large part of the test was made up of 5–10 μ pyrite, and in the *pectinatus* zone the amount rose to 50 per cent. Again, in the *pallasioides* zone there was an increase in the grain size, with specimens using a mixture of 10–30 μ quartz and a little 5 μ pyrite.

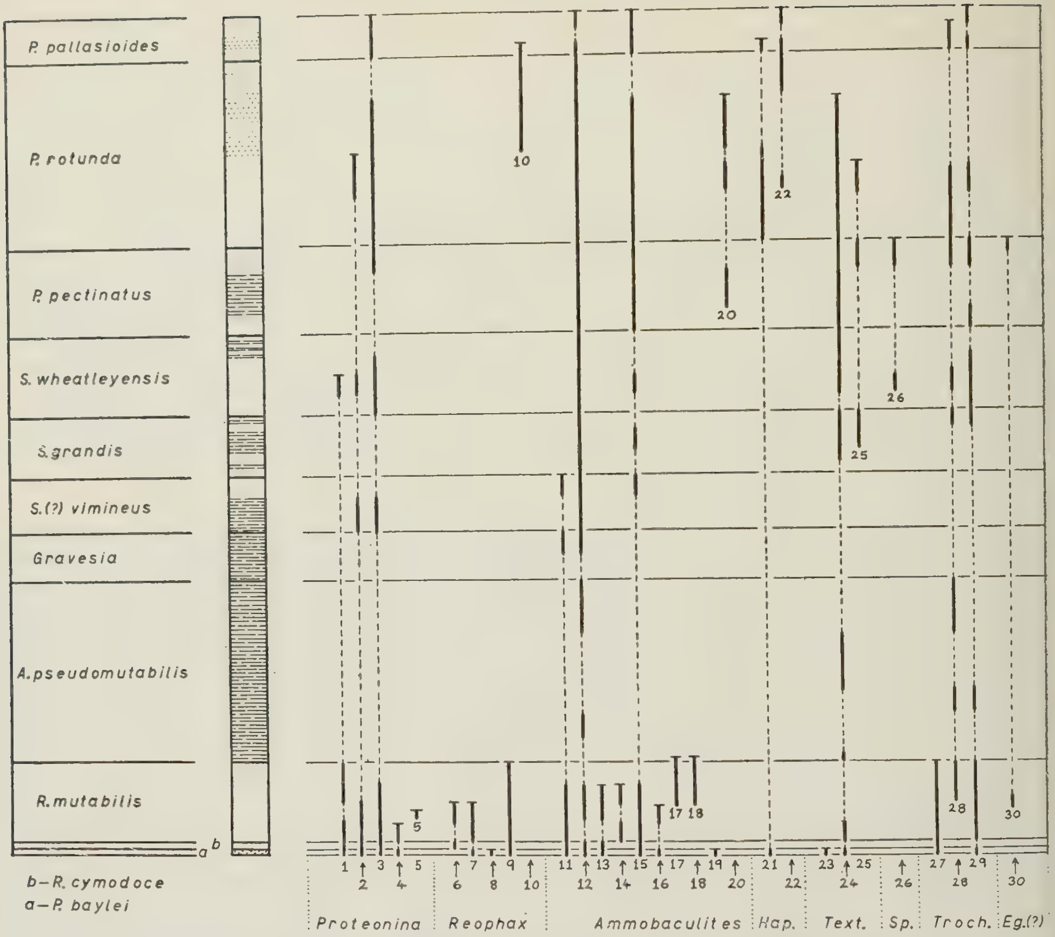
From the *pseudomutabilis* zone to the *pectinatus* zone *Textularia jurassica* (Gümbel) agglutinated fine-grain material. For most of the range pyrite alone was used but towards the top some 10 μ garnet and quartz were added as minor constituents. This dominance of pyrite is in marked contrast to the species described above, where it rarely makes up more than half of the test and is usually present to a much smaller degree.

Trochammina globigeriniformis (Parker and Jones) agglutinated medium-grained quartz in the *baylei* zone and fine-grained quartz in the *mutabilis* zone, but by the *pseudomutabilis* zone only pyrite was agglutinated. Through the *Subplanites* zone pyrite of 5–15 μ grade dominated but in the *pectinatus* zone more than 50 per cent. of the test in some specimens was made up of fine-grained quartz. In the *Pavlovia* zones quartz was usually dominant, though with up to 50 per cent. pyrite present, but there was no increase in grain size in the upper part.

(*b*) Variation in the short-range forms. In the *baylei* zone the grain size utilized was, in general, coarser than in the later zones, but *Ammobaculites laevigatus* Lozo, a large form apparently confined to this zone, agglutinated only fine-grained quartz. *Ammobaculites* cf. *coprolithiformis* (Schwager) occurred in the same zone, where its test was composed of many large quartz grains in a 30 μ quartz matrix, and in the *mutabilis* zone where large shell fragments replaced the large quartz grains. *Ammobaculites subaequalis* Myatliuk and *Ammobaculites braunsteini* Cushman and Applin, large forms present in the upper part of the *mutabilis* zone, used only medium-grained quartz. From these four cases it would appear that there is no correlation between the coarseness of material employed and the size of the adult foraminifera.

Two forms restricted to the sandy clays at the top of the *Pavlovia* zones again show contrasting characters. *Reophax hounstoutensis* sp. nov. used coarse-grain material, dominantly 70–80 μ quartz with occasional larger grains. Over 90 per cent. of the material is yellow quartz with only a small amount of clear and white quartz. This gave the species a very uniform appearance both as to grain size and colour. *Haplophragmoides haeusleri* sp. nov. was similar in using a grain size in the 70–100 μ range but appeared to be much more 'fashion conscious'. Individual specimens employed a variety of colour schemes by combining two or rarely three of the available coloured quartzes. Yellow and clear, grey with subordinate clear, yellow with few glauconite grains and yellow, subordinate clear and rare garnet were some of the more common fashions. A colour scheme, once decided upon, was adhered to throughout the test with great constancy. There is, therefore, a definite selective capacity as regards both colour and grain size, but while the grain size is a character uniform to the whole species the choice of colour was a matter of individual discretion. Such cases of colour selectivity can be seen in many other species.

(*c*) Conclusions. 1. Grain size is the most important single character but long-ranging species, perhaps by their very nature, can tolerate somewhat restricted changes in the size used.



TEXT-FIG. 2. Table showing ranges of arenaceous foraminifera in the Kimeridgian.

1, *Proteonina difflugiformis* A. 2, *P. difflugiformis* B. 3, *P. difflugiformis* C. 4, *P. difflugiformis* D. 5, *P. conferrens*. 6, *Reophax sterkii*. 7, *R.* cf. *variabilis*. 8, *R. scorpiurus*. 10, *R. hounstoutensis*. 11, *Ammobaculites agglutinans* A. 12, *A. agglutinans* B. 13, *A. agglutinans* C. 14, *A.* cf. *hockleyensis*. 15, *A. deceptorius*. 16, *A.* cf. *coprolithiformis*. 17, *A. subaequalis*. 18, *A. braunsteini*. 19, *A. laevigatus*. 20, *A. sp. juv*. 21, *Haplophragmoides latidorsatum*. 22, *H. haeusleri*. 23, *Textularia agglutinans*. 24, *T. jurassica*. 25, *T. auensteinensis*. 26, *Spiroplectammina biformis*. 27, *Trochammina squamata*. 28, *T.* cf. *nitida*. 29, *T. globigeriniformis*. 30, *Eggerella? meentzeni*.

2. Quartz or ‘quartz substitute’ (glauconite, garnet, &c.) is the preferred material for many species with medium and coarse-grained tests.

3. Pyrite is an important element only in species with fine-grained tests, either: (*a*) In species such as *T. jurassica* where it is the preferred material. (*b*) In species such as *T. globigeriniformis* where the preferred material is fine-grained quartz, but pyrite is readily acceptable as a substitute and may occur in amounts over 50 per cent. (*c*) In some fine-medium grain forms where quartz is the preferred material a slight change in grain size may bring the species into the pyrite range. Then pyrite is accepted with varying degrees of reluctance and rarely exceeds 50 per cent. of the total amount.

4. Shell fragments were utilized only once, in sample Do-Mu 3, but in this case, of the eight species recorded, one, *Proteonina conferrens* sp. nov. used it as a preferred material and appears to be restricted to this sample, *A.* cf. *coprolithiformis* used it as a coarse-grained material in the absence of a suitable size of quartz, as did *Reophax sterkii* Haeusler 1890. Two medium-grained forms, *P. difflugiformis* and *A. agglutinans*, employed it as a subordinate material, and the three fine-grained forms, *A. deceptorius*, *T. globigeriniformis*, and *Eggerella(?) meentzeni* (Klingler), did not use it. There is clear correlation here between grain size and usage, but this cannot be the only factor or shell fragments would have been more widely used.

5. Selection for colour is made by individuals and is not, of necessity, a specific character.

6. Echinoderm and fish remains were rarely used, due probably to their prohibitive size.

7. '*Inoceramus*' prisms were used as a minor constituent in one species, *P. difflugiformis*, in one sample, Do-Pa 2. Wider usage was not restricted by non-availability.

Hofker (1953) considered that each species chose its material for agglutinating as a genetic character of the species. He thought that the size, chemical composition, and shape of the particles were equally important. In contrast to these conclusions, based on observations from a large part of the geological column, Slama (1954) reported laboratory experiments on species of *Ammobaculites*. His specimens agglutinated all sizes of material from silt grade, forming the substratum of their natural environment, to the coarse quartz of the laboratory tank, but when 500 grade Carborundum was available, agglutinated this in preference to coarser materials. The results of the present study agree with those of Hofker; no parallel to Slama's observations could be seen.

SYSTEMATIC DESCRIPTIONS

Proteonina difflugiformis (Brady)

Plate 54, figs. 1–4

Reophax difflugiformis Brady 1879, p. 51, pl. 4, fig. 3.
Haplophragmium lagenarium Berthelin 1880, p. 21, pl. 1, fig. 2.
Reophax scorpiurus Montfort, Haeusler 1883*b*, p. 27, pl. 2, fig. 7.
Reophax difflugiformis Brady, Haeusler 1890, p. 26, pl. 3, figs. 1, 2; pl. 5, figs. 25–27.
Proteonina difflugiformis (Brady), Paalzow 1917, p. 15.
Proteonina compressa Paalzow 1932, p. 90, pl. 4, figs. 2, 3.
Proteonina ampullacea (Brady), Franke 1936, p. 13, pl. 1, figs. 7*a*, *b*.
Proteonina difflugiformis (Brady), Bartenstein and Brand 1937, p. 128, pl. 1*a*, fig. 1; pl. 1*b*, figs. 1, 2; pl. 2*a*, fig. 1; pl. 2*b*, fig. 3; pl. 3, fig. 1; pl. 4, fig. 1; pl. 5, fig. 1; pl. 6, figs. 2*a*, *b*; pl. 8, figs. 1*a*–*d*; pl. 10, figs. 1*a*–*c*; pl. 11*a*, figs. 1*a*–*c*.
Proteonina ampullacea (Brady), Bartenstein and Brand 1937, p. 128, pl. 8, figs. 2*a*, *b*; pl. 10, figs. 2*a*, *b*.

Description. Test egg-shaped to flask-shaped in lateral view, circular or somewhat compressed in cross-section. The agglutinated material is usually 40–60 μ quartz though some shell fragments and pyrite may be included. The grains are close set with little silicious cement. The aperture is simple, terminal, varies in shape with the cross-section of the test and may have an associated neck.

Remarks. Variation occurs both in the lateral outline, particularly the development of the apertural neck, and in the cross-section. Four stages have been selected to illustrate the former. Variant A (Pl. 54, fig. 1) has an egg-shaped test with no marked narrowing towards the aperture; B (Pl. 54, fig. 3) has its aperture at the apex of a cone which forms half or more of the test; C (Pl. 54, fig. 2) has a test consisting of a sub-spherical body chamber with a distinct, short neck, and D (Pl. 54, fig. 4) is a slender form with a long neck and a flared lip to the aperture. The mode for the species falls between B and C. The extremes were rare and almost unknown above the Lower Kimeridgian.

Jurassic forms of *Proteonina* with a circular cross-section have usually been identified with *P. difflugiformis* (Brady) but the compressed (or possibly squashed) forms have often been referred to different species. Thus Paalzow (1932) placed such forms in *P. compressa* sp. nov., and both Franke (1936) and Bartenstein and Brand (1937) referred similar specimens to *P. ampullacea* (Brady). Parker and Phleger (1951) have shown that in some Recent species there is primary compression of the test, yet in fossil specimens from argillaceous rocks it would be unwise to speciate solely on this criterion. The Kimeridgian specimens showed all intermediates between a circular and a completely squashed cross-section.

Specimens of *Reophax difflugiformis* from the Brady Collection, all labelled syntypes, are preserved on three slides in the British Museum (Natural History). ZF 2267 has five specimens of which one was figured. All are small forms with a slender neck and agglutinated fine quartz grains. The single specimen on ZF 2268 is larger and agglutinated sponge spicules. In addition to this 'Challenger' material there are twenty-nine specimens collected on the 'Porcupine' expedition and mounted on slide ZF 2269. These forms are nearly twice the size of those on ZF 2267 and agglutinated medium quartz grains in a way that left the outer surface rough. The 'Challenger' specimens may not be conspecific with the 'Porcupine' specimens, which agree well with the Kimeridgian material.

Proteonina conferrens sp. nov.

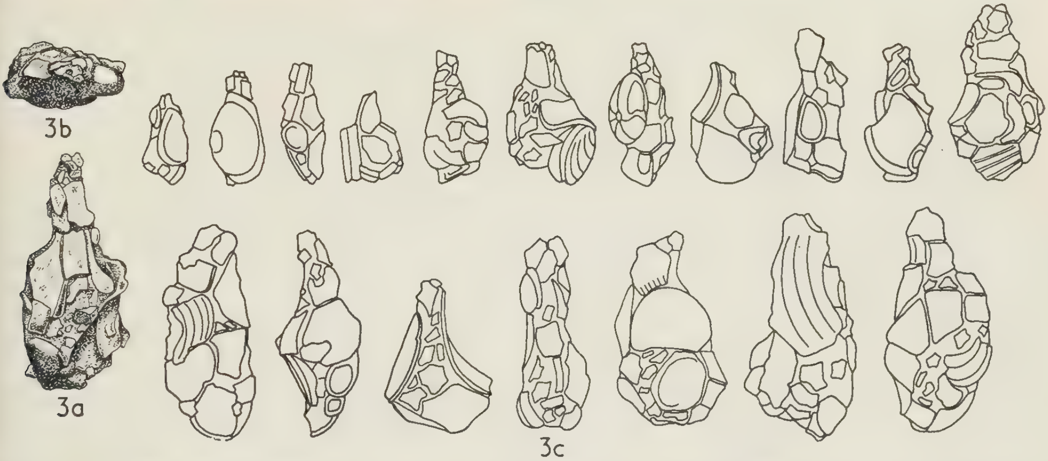
Plate 54, fig. 5; text-fig. 3

Diagnosis. Test sub-ovoid to flask-shaped, often elongate. Cross-section round to compressed. Agglutinated material large shell fragments, frequently cemented edge to edge with little cement (type not ascertained). Small shell fragments and quartz grains used to a minor degree. The aperture is small, circular, terminal, often with a slender neck.

Type locality and horizon. Thirty-five ft. above the base of the *mutabilis* zone of Black Head, near Osmington Mills, Dorset. Grid Ref. 30/727.818. Sample Do-Mu 3.

Remarks. This species, owing to its habit of agglutinating large shell fragments, is variable in shape (Paratypes—text-fig. 3), but certain trends are common. The test is usually at least twice as long as it is broad, and curved shell fragments are often mounted with the concave side out, particularly in the region of the aperture so that a slender neck is not unusual. Fragments of lamellibranch and ammonite shells are the usual material but young lamellibranchs, gastropods, ostracods, and other foraminifera may be included. Quartz grains occur in small quantities, a marked difference to *P. difflugi-*

formis from the same horizon where quartz is dominant and broken shell fragments rare. *P. conferrens* was confined to a single sample (Do-Mu 3), represented by eighty-six specimens, with the original cement replaced by pyrite in all cases.



TEXT-FIG. 3. *Proteonina conferrens* sp. nov. 3*a*, *b*, Lateral and apertural views of holotype, P. 43982 (see Pl. 54, fig. 5), ×42·5. 3*c*, Camera lucida drawings of paratypes, P. 43983, ×36; *mutabilis* zone, Black Head, near Osmington Mills, Dorset.

Reophax sterkii Haeusler

Plate 54, figs. 6*a*, *b*

Reophax sterkii Haeusler 1890, p. 26, pl. 3, fig. 23.

Description. The slightly compressed test consists of three or four chambers in a straight or gently curved series. Early chambers are wider than high, the end chamber tapers to a broad apertural neck and makes up more than half of the test. The sutures are indistinct. The agglutinated material is 80–100 μ quartz in the *cymodoce* zone but in the *mutabilis* zone it is 60 per cent. large shell fragments and 40 per cent. fine-medium quartz. The aperture is simple, circular to oval, terminal.

Remarks. Recent species of similar form have either been placed as varieties of *R. scorpiurus* Montfort or referred to new species, as were *R. curtus* Cushman 1920 and *R. subfusiformis* Earland 1933. Both authors extracted figures from *R. scorpiurus* Montfort, Goes 1894, and Hoglund (1947, pp. 77–86) considers these new species synonymous. The only similar form described from Jurassic rocks is *R. sterkii.* This species was seen in the *cymodoce* and *mutabilis* zones.

Reophax cf. *variabilis* Herrmann 1917 *non* Haeusler 1885.

Plate 54, fig. 13

Cf. *Reophax variabilis* Herrmann 1917, p. 286, pl. 2, figs. 19*a–c*.

Description. The test consists of three or four globose chambers in a straight or curved series. Each chamber is wider than high in lateral view and circular in cross-section. The agglutinated material is 40–60 μ quartz grains, set separately in a fine, white, calcareous cement. The aperture is simple, circular, terminal, sometimes with a short neck. Occurs rarely in the *mutabilis* zone.

Reophax scorpiurus de Montfort

Plate 54, fig. 15

Reophax scorpiurus de Montfort 1808, p. 331, fig. on p. 330.
Nodulina scorpiurus (Montfort), Paalzow 1917, p. 18, pl. 41, fig. 10.

Description. The test consists of a sub-linear series of five or six elongate chambers, circular in cross-section, separated by distinct, depressed sutures. Successive chambers show a gradual increase in height and breadth. The agglutinated material is 20–40 μ quartz with a little pyrite set in a calcareous cement. The aperture is simple, circular and terminal. Occurs rarely in the *baylei* zone.

Reophax helvetica Haeusler

Plate 54, fig. 8

Dentalina helvetica Haeusler 1881, p. 34, pl. 2, fig. 45.
Reophax helvetica Haeusler 1883*b*, p. 27, pl. 2, figs. 8–10.
Reophax helvetica Haeusler 1890, p. 28, pl. 3, figs. 15–17.
Nodulina compressa Paalzow 1917, p. 18, pl. 41, figs. 11, 12.
Reophax agglutinans (Terquem), Paalzow 1932, p. 92, pl. 4, figs. 8, 9.
Reophax multilocularis Haeusler, Bartenstein and Brand 1937, p. 133, pl. 5, fig. 8; pl. 6, fig. 9; pl. 8, figs. 8*a*, *b*; pl. 10, fig. 9; pl. 11*a*, fig. 5; pl. 15*a*, fig. 4; pl. 15*c*, fig. 2.

Description. The test is a linear series of three to five chambers, each sub-rectangular in lateral view and with a slightly compressed, oval cross-section. The sutures are straight and gently depressed. The agglutinated material is 15–40 μ quartz with a little pyrite sometimes included. The aperture is simple, circular, terminal, rarely set on a short, thick neck.

Remarks. In lateral view the margins of most forms diverge at a low angle. Those in which the angle of divergence is higher approach *R. metensis* Franke 1936 which is otherwise distinct. This species is frequent from the *baylei* zone to the middle of the *mutabilis* zone.

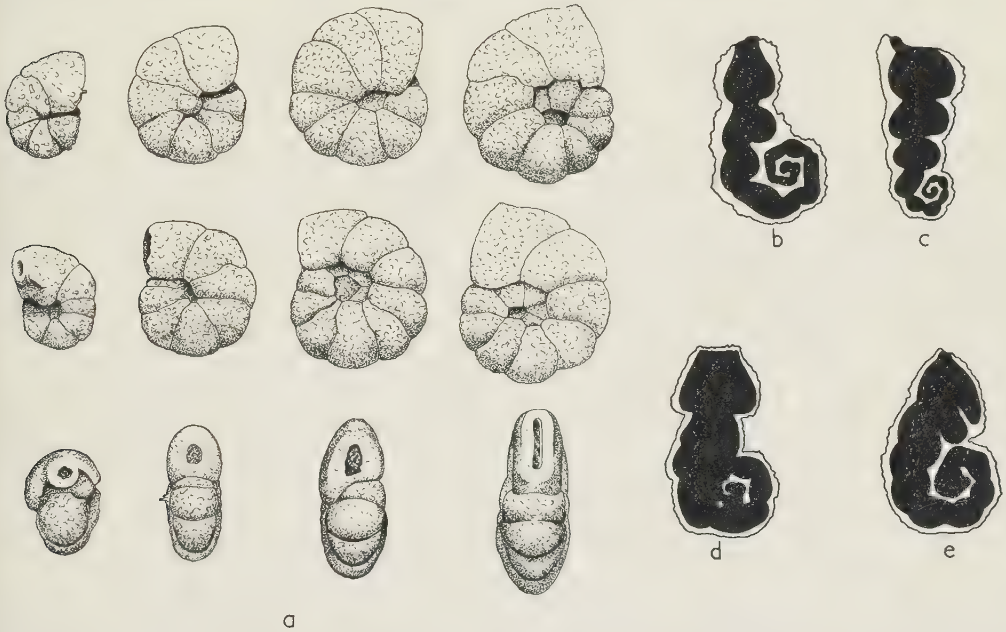
Reophax hounstoutensis sp. nov.

Plate 54, figs. 7*a*, *b*; text-figs. 5*d*, *e*

Diagnosis. The test is a rectilinear series of four to seven chambers. The proloculum is large and sub-spherical, the second chamber wider than high. More distal chambers become progressively wider but their heights remain the same. The sutures are depressed but due to the coarse grain size are indistinct. Agglutinated material is 70–80 μ quartz with occasional larger grains, closely packed with a little calcareous cement. The outer surface is extremely rough. In all the specimens examined no trace of an aperture could be found anywhere on the test.

Type locality and horizon. Near the top of the *Rhynchonella* Marls (*rotunda* zone) of Hounstout, near Kingston, Dorset. Grid ref. 30/950773. Sample Do-Pa 15.

Remarks. This species was rare in the upper part of the *Rhynchonella* Marls and in the Hounstout Clay. Some variation occurred in the angle of divergence of the margins when seen in lateral view. Only one size of proloculum was observed.



TEXT-FIG. 4. *Ammobaculites spp.* 4*a*, Obverse, reverse, and apertural views of four specimens, showing the ontogeny of *A. laevigatus* Lozo, P. 43968–71, ×34; *baylei* zone, Black Head, near Osmington Mills, Grid ref. 30/727818. 4*b–e*, Pyrite-infilled specimens immersed in clove oil and drawn by transmitted light. 4*b*, *A. agglutinans* A, P. 43961, ×47. 4*c*, *A. agglutinans* B, P. 43960, ×36. 4*d*, *A. agglutinans* C, P. 43959, ×55. 4*e*, *A.* cf. *hockleyensis*, P. 43962, ×65.

Ammobaculites agglutinans (d'Orbigny)

Plate 54, figs. 9–11; text-figs. 4*b–d*

Spirolina agglutinans d'Orbigny 1846, p. 137, pl. 7, figs. 10–12.
Haplophragmium coprolithiforme Schwager, Paalzow 1922, p. 31, pl. 5, fig. 3.
Ammobaculites coprolithiformis (Schwager), Paalzow 1932, p. 94, pl. 4, fig. 19.
Ammobaculites agglutinans (d'Orbigny), Bartenstein and Brand 1937, p. 186, pl. 4, fig. 14; pl. 5, fig. 78; pl. 6, figs. 40*a*, *b*; pl. 8, figs. 38*a–c*; pl. 10, figs. 45*a*, *b*; pl. 11*a*, figs. 19*a*, *b*; pl. 12*a*, fig. 22; pl. 13, fig. 23; pl. 14*b*, fig. 19.
Ammobaculites infravolgensis Myatliuk 1939, p. 45, pl. 2, figs. 17*a*, *b*, 18.
Ammobaculites agglutinans (d'Orbigny), Bielecka and Pozaryski 1954, p. 158, pl. 2, figs. 3*a–c*.

Description. The test is an evolute, planispiral coil of two whorls, with five or six chambers in the last whorl, followed by two to four chambers in a rectilinear, uncoiled series. Sutures and umbilicus may be indistinct but are usually depressed. The preferred material agglutinated is 20–40 μ quartz, but fine quartz with subordinate pyrite may be used. The cement is calcareous. In the adult the aperture is circular and central in the terminal face of the end chamber.

Remarks. Variation occurs in the tightness of coiling, amount of depression of the sutures and umbilicus, and to a lesser extent in the size of the coil and chamber shape. Three variants are distinguished. Of the three, A (Pl. 54, fig. 9; text-fig. 4*b*) has the most evolute coil but the umbilicus is not well defined and the sutures are depressed only in the linear part. This common variant from the *baylei* zone to the middle of the *mutabilis* zone becomes infrequent later. The circular cross-section of the linear part allows it to be separated from the otherwise similar *A.* cf. *hockleyensis*. Variant B (Pl. 54, fig. 10; text-fig. 4*c*) also has an evolute coil but the umbilicus is distinct and all sutures in the last whorl of the coil and the uncoiled part are depressed. This, the most common variant, occurs throughout the Kimeridgian. Variant C (Pl. 54, fig. 11; text-fig. 4*d*) is more involute than the others but has a small, deep umbilicus; all sutures are depressed and in the linear part the chambers are widest near their proximal sutures; it occurs only in the *baylei*, *cymodoce*, and *mutabilis* zones.

Spirolina agglutinans, though a Tertiary form from the Vienna Basin was figured and described as close to the Kimeridgian specimens. Similar forms originally described from the Jurassic are *A. infravolgensis* Myatliuk, which differs only in having five or six chambers in the coil, and *A. suprajurassicus* (Schwager) as revised by Seibold and Seibold (1956, p. 105, text-fig. 3*h*; pl. 7, fig. 16). The latter differs only in minor respects and should, perhaps, be considered synonymous with the present form.

Ammobaculites cf. *hockleyensis* Cushman and Applin

Plate 54, fig. 19; text-fig. 4*e*

Cf. *Ammobaculites hockleyensis* Cushman and Applin 1926, p. 163, pl. 6, fig. 2.

Description. The test consists of an evolute, planispiral coil of two whorls followed by a short, laterally compressed uncoiled part of two chambers. The agglutinated material is 20–40 μ quartz, close set in a calcareous cement. The aperture is simple, terminal, a short slit at the apex of the end chamber.

Remarks. The species described by Cushman and Applin (1926) from the Jackson Formation (Up. Eocene) differs only in its involute coil, however, the Kimeridgian specimens also appeared involute till they were immersed in clove oil. Occurs rarely in the *mutabilis* zone.

Ammobaculites deceptorius (Haeusler)

Plate 54, figs. 24*a*, *b*

Reophax sp. indet. Haeusler 1890, p. 30, pl. 3, fig. 13.
Bigenerina deceptoria Haeusler 1890 (pars), p. 74, pl. 12, figs. 11–13.
Ammobaculites praelonga ten Dam 1944, p. 80, pl. 6, fig. 9.

Description. The initial 'coil' consists of two globular chambers placed side by side, and is followed by three to six chambers in a straight or gently curved series. The linear chambers are globular with depressed, transverse sutures, and a circular cross-section. The distal end of the last chamber is drawn out into a stout apertural neck. The agglutinated material is fine-grained quartz or globular pyrite. The aperture is simple, round, terminal, mounted on a neck, central in the terminal face of the last chamber. Occurs commonly from the *baylei* to *mutabilis* zones and from the *vimineus* sub-zone to the top of the formation.

Ammobaculites cf. *coprolithiformis* (Schwager)

Plate 54, figs. 12*a*, *b*

Cf. *Haplophragmium coprolithiforme* Schwager 1867, p. 654, pl. 34, fig. 3.

Description. A small evolute coil of two whorls, the whorl height increasing rapidly, is followed by a rectilinear series of four or five chambers, each wider than high and wider parallel to the axis of coiling than normal to it. The sutures are gently depressed in the linear part but indistinct in the coil. The agglutinated material is coarse quartz or shell fragments up to 240 μ in diameter, set in a matrix of 30 μ quartz which itself has a calcareous cement. The aperture is simple, round, terminal.

Remarks. This species is rare in the *baylei* and *mutabilis* zones.

Ammobaculites subaequalis Myatliuk

Plate 54, figs. 16, 17

Ammobaculites subaequalis Myatliuk 1939, p. 44, pl. 2, figs. 19, 20.

Description. The large test consists of an involute coil with four or five chambers in the last whorl, followed by an uncoiled part of one or two chambers. The sutures are depressed, radial in the coil, and nearly transverse in the linear part. The inflated chambers in the coil are followed by the first uncoiled chamber, twice the size of its predecessor, which in turn is followed by a sub-globular end chamber with a short, stout apertural neck. The agglutinated material is 40–60 μ quartz grains, closely set with little calcareous cement. The aperture is simple, circular, mounted on a neck, central in the terminal face of the end chamber.

Remarks. This form was common from the middle of the *mutabilis* zone to the base of the *pseudomutabilis* zone. It always occurred with *A. braunsteini*.

Ammobaculites braunsteini Cushman and Applin

Plate 54, figs. 20, 21

Ammobaculites braunsteini Cushman and Applin 1946, p. 76, pl. 13, figs. 7*a*, *b*.
Ammobaculites braunsteini Cushman and Applin, Bielecka and Pożaryski 1954, p. 160, pl. 2, figs. 5*a*, *b*.

Description. The large test consists of an involute coil with six or seven chambers in the last whorl and a deep but narrow umbilicus, followed by one or two uncoiled chambers. The sutures are depressed, sub-radial in the coil where they may be sinuous, always

EXPLANATION OF PLATE 54

All figures ×33. The specimens are in the British Museum (Natural History).

Figs. 1–4. *Proteonina difflugiformis* (Brady). 1, Variant A, *baylei* zone, P. 43951, length 0·28 mm., max. width 0·21 mm. 2, Variant C, *cymodoce* zone, P. 43953, length 0·38 mm., max. width 0·25 mm. 3, Variant B, *cymodoce* zone, P. 43952, length 0·43 mm., max. width 0·25 mm. 4, Variant D, *baylei* zone, P. 43954, length 0·49 mm., max. width 0·21 mm.

Fig. 5. *Proteonina conferrens* sp. nov., holotype, *mutabilis* zone, P. 43982, length 0·74 mm., max. width 0·36 mm.

Fig. 6*a*, *b*. Lateral view and clove-oil 'section' of *Reophax sterkii* Haeusler, *cymodoce* zone, P. 43955, length 0·72 mm., max. width 0·40 mm.

Fig. 7. *Reophax hounstoutensis* sp. nov., holotype, *Rhynchonella* Marls, *rotunda* zone, P. 43984, length 1·0 mm., max. width 0·47 mm.; *a*, lateral view; *b*, chamber arrangement.

Fig. 8. *Reophax helvetica* Haeusler, *mutabilis* zone, P. 43958, length 0·78 mm., max. width 0·25 mm.

Figs. 9–11. *Ammobaculites agglutinans* (d'Orbigny). 9, Variant A, *baylei* zone, P. 43961, length 1·0 mm., width of coil 0·32 mm. 10, Variant B, Crushed Ammonoid Shales, *rotunda* zone, P. 43960, length 0·69 mm., width of last chamber 0·28 mm., width of coil 0·24 mm. 11, Variant C, *baylei* zone, P. 43959, length 0·45 mm., width of coil 0·22 mm.

Fig. 12*a*, *b*. Lateral view and clove-oil 'section' of *Ammobaculites* cf. *coprolithiformis* (Schwager), *baylei* zone, P. 49364, length 1·05 mm., width of coil 0·38 mm.

Fig. 13. *Reophax* cf. *variabilis* Herrmann, *mutabilis* zone, P. 43956, length 0·69 mm., max. width 0·36 mm.

Fig. 14. *Ammobaculites laevigatus* Lozo, *baylei* zone, P. 43971, height 0·71 mm., width 0·62 mm.

Fig. 15. *Reophax scorpiurus* Montfort, *baylei* zone, P. 43957, length 0·62 mm., max. width 0·18 mm.

Figs. 16, 17. *Ammobaculites subaequalis* Myatliuk, *mutabilis* zone. 16, Young form, height 0·60 mm., width 0·50 mm., P. 43966. 17, Adult, P. 43967, height 1·08 mm., width 0·56 mm.

Fig. 18. *Ammobaculites sp. juv.*, *pectinatus* zone, P. 43972, height 0·29 mm., width 0·26 mm.

Fig. 19. *Ammobaculites* cf. *hockleyensis* Cushman and Applin, *mutabilis* zone, P. 43962, length 0·39 mm., width of coil 0·25 mm.

Figs. 20, 21. *Ammobaculites braunsteini* Cushman and Applin, *pseudomutabilis* zone. 20, Young form, P. 43965, height 1·13 mm., width 1·03 mm. 21, Adult, P. 43986, height 2·13 mm., width of coil 1·34 mm.

Fig. 22. *Haplophragmoides haeusleri* sp. nov., holotype, *Rhynchonella* Marls, *rotunda* zone, P. 43985, height 0·89 mm., width 0·69 mm.

Fig. 23*a*, *b*. Lateral and apertural views of *Haplophragmoides latidorsatum* (Bornemann), Crushed Ammonoid Shales, *rotunda* zone, P. 43973, height 0·29 mm., width 0·26 mm.

Fig. 24*a*, *b*. Lateral view and clove-oil 'section' of *Ammobaculites deceptorius* (Haeusler), Crushed Ammonoid Shales, *rotunda* zone, P. 43963, length 0·64 mm., width of last chamber 0·21 mm.

Fig. 25. *Textularia agglutinans* d'Orbigny, *baylei* zone, P. 43974, length 0·39 mm., max. width 0·19 mm.

Fig. 26. *Textularia jurassica* (Gümbel), Crushed Ammonoid Shales, *rotunda* zone, P. 43975, length 0·36 mm., max. width 0·14 mm.

Fig. 27. *Textularia auensteinensis* (Haeusler), *pectinatus* zone, P. 43976, length 0·39 mm., max. width 0·11 mm.

Fig. 28. *Spiroplectammina biformis* (Parker and Jones), *wheatleyensis* zone, P. 43977, length 0·47 mm., max. width 0·15 mm., width of coil 0·10 mm.

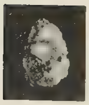
Fig. 29. *Trochammina squamata* Jones and Parker, *baylei* zone, P. 43978, max. diameter 0·32 mm.

Fig. 30. *Trochammina* cf. *nitida* Brady, Crushed Ammonoid Shales, *rotunda* zone, P. 43979, max. diameter 0·32 mm.

Fig. 31. *Trochammina globigeriniformis* (Parker and Jones), *pectinatus* zone, P. 43980, max. diameter 0·18 mm.

Fig. 32. *Eggerella? meentzeni* (Klingler), *mutabilis* zone, P. 43981, height 0·27 mm., max. width 0·22 mm.

Localities. Figs. 1–6, 8, 9, 11–17, 19–21, 25, 29, 32 from Black Head, near Osmington Mills, Dorset, Grid ref. 30/727818. Figs. 7, 10, 22–24, 26, 27, 30 from Hounstout, near Kingston, Dorset, Grid ref. 30/947773. Figs. 18, 31 from Freshwater Steps, near Kingston, Dorset, Grid ref. 30/942773. Fig. 28 from Rope Lake Head, near Kimeridge, Dorset, Grid ref. 30/927775.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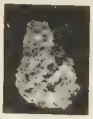
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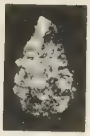
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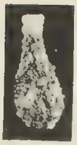
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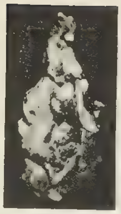
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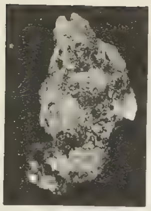
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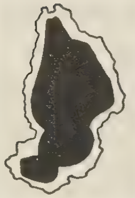
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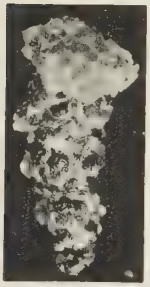
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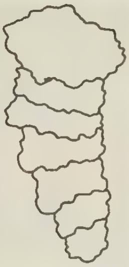
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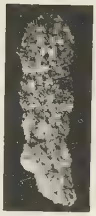
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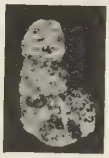
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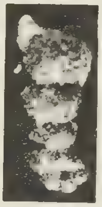
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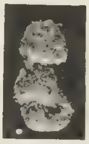
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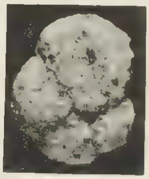
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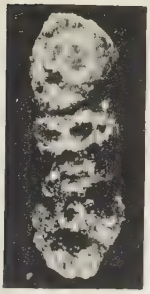
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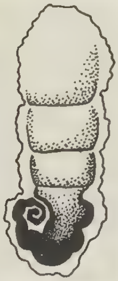
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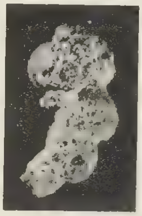
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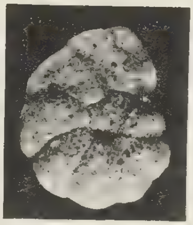
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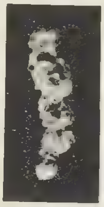
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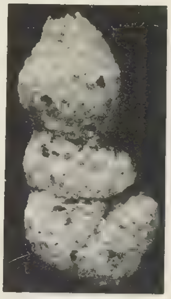
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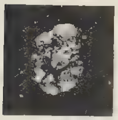
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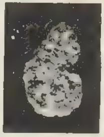
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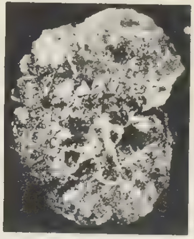
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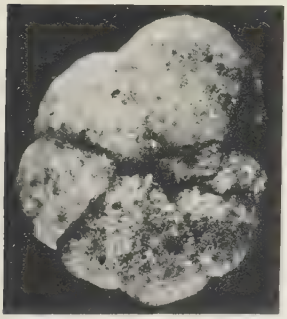
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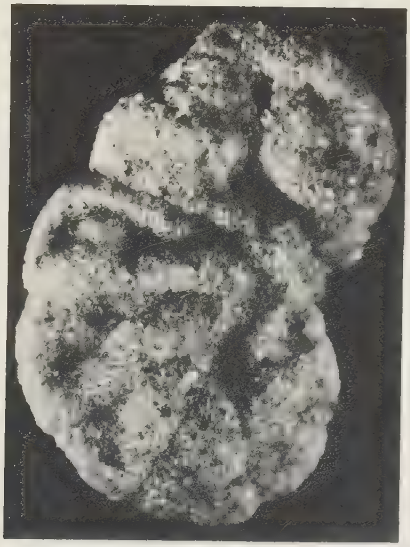
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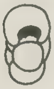
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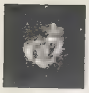
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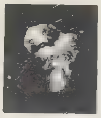
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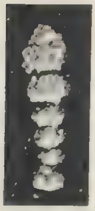
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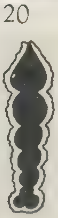
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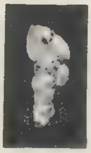
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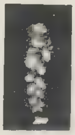
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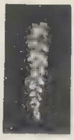
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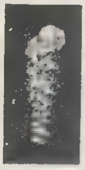
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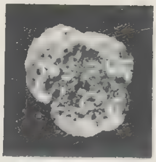
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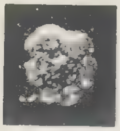
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sinuous in the linear part. The cross-section of the coil chambers is sub-triangular with a narrow, but rounded, periphery; that of the linear chambers oval. Agglutinated material is 20–60 μ quartz, closely set with little calcareous cement. The aperture is simple, central in the terminal face and appears to be oval, though the shape has often been distorted by crushing.

Remarks. A. braunsteini has a similar range to *A. subaequalis* from which it can be separated by the greater number of chambers in the coil, absence of an apertural neck; sinuous sutures and an oval aperture, though the latter two characters may owe their origin to the crushed nature of all specimens found.

Ammobaculitus laevigatus Lozo

Plate 54, fig. 14; text-fig. 4*a*

Ammobaculites laevigata Lozo 1944, p. 539, pl. 2, figs. 2, 3; text-figs. 14*a–h*.

Description. The test consists of a coil of three or four whorls, the early whorls involute with seven or eight chambers each. The later whorls, with nine or ten chambers each, become increasingly evolute and asymmetrical so that more of the early chambers is exposed on one side than the other. The depressed sutures are radial in the initial stages but later are recurved to the lobulate periphery. A few specimens have an uncoiled part of one laterally compressed chamber. The agglutinated material is fine-grained quartz with little calcareous cement. The aperture is simple and central in the terminal face of the last chamber, circular in the young form, becoming a median slit in the adult. The ontogeny is shown on text-fig. 4*a*.

Remarks. A. laevigatus was common in the lowest foot of the *baylei* zone.

Ammobaculites sp. juv.

Plate 54, fig. 18

Description. The test is a small evolute coil of three whorls with seven chambers in the last whorl. Early chambers are sub-quadrate in cross-section, later they are sub-triangular. The depressed sutures are recurved. The agglutinated material is fine-grained quartz with little calcareous cement. The aperture is a low arch at the base of the terminal face.

Remarks. This form is similar to the juveniles of *A. agglutinans* but differs in still having a basal aperture where *A. agglutinans*, at the same size, has a central aperture. No corresponding adult was seen. Occurred rarely in the middle of the *pectinatus* zone and in the *rotunda* zone.

Haplophragmoides latidorsatum (Bornemann)

Plate 54, figs. 23*a*, *b*

Nonionina latidorsata Bornemann 1855, p. 339, pl. 16, fig. 4.
Haplophragmium latidorsatum (Bornemann), Haeusler 1890, p. 35, pl. 3, figs. 37, 38.
Haplophragmoides subglobosus (G. O. Sars), Bartenstein and Brand, p. 188, pl. 4, fig. 12.

Description. The test is an involute planispiral coil with five or six chambers in the last whorl. All chambers are globular, early chambers sub-circular in cross-section, adult chambers higher than wide but still with a rounded periphery. The sutures are depressed and radial. The agglutinated material is fine-grained quartz with a calcareous cement. The semicircular aperture is basal on the terminal face of the end chamber.

Remarks. This species was rare in the *baylei* zone, but frequent from the base of the *rotunda* zone to the top of the Hounstout Clay.

Haplophragmoides haeusleri sp. nov.

Plate 54, fig. 22; text-figs. 5*i, j*

Diagnosis. The test is an involute planispiral coil with five to six chambers in the last whorl. In axial section early chambers are sub-circular but later chambers are compressed with a rounded periphery. The sutures are radial, depressed, but obscured by the coarse grain size. The agglutinated material is 70–100 μ quartz with occasional glauconite and red garnet, close set with little calcareous cement. The aperture is semicircular, basal on the terminal face of the end chamber, with its peripheral margin clearly defined by a ring of 40 μ quartz grains.

Type locality and horizon. Near the top of the *Rhynchonella* Marls (*rotunda* zone) of Hounstout, near Kingston, Dorset. Grid ref. 30/950773. Sample Do-Pa 15.

Remarks. This species can be distinguished from *H. latidorsatum* (Born.) by its coarser-grained size, larger overall size, the more compressed cross-section and less lobate periphery of the adult chambers. It occurs rarely in the Crushed Ammonoid Shales and frequently from the middle of the *Rhynchonella* Marls to the top of the Hounstout Marls.

Textularia agglutinans d'Orbigny

Plate 54, fig. 25

Textularia agglutinans d'Orbigny 1839, p. 144, Plates vol. 8, pl. 1, figs. 17, 18, 32–34.
Textilaria jurassica Gümbel, var. *maxima* Haeusler 1881, p. 36, pl. 2, fig. 50.
Textularia agglutinans d'Orbigny, Haeusler 1890 (pars), p. 71, pl. 11, figs. 1–9, 47, 50, 52.

Description. In lateral view the margins of the biserial part diverge at an angle between 20° and 30°. The chamber size increases rapidly, the early chambers are wider than high, distal chambers may be as high as wide. The sutures are depressed and lateral sutures are normal to the long axis of the test. The agglutinated material is fine-grained quartz with little calcareous cement. The aperture is a high arch, basal on the terminal face.

Remarks. This species of *Textularia* is the largest in the Kimeridgian. The test is often twisted about its long axis through 90° or more. Occurs frequently in the *baylei* zone.

Textularia jurassica (Gümbel)

Plate 54, fig. 26

Textilaria jurassica Gümbel 1862, p. 228, pl. 4, fig. 17.
Textilaria franconica Gümbel 1862, p. 229, pl. 4, fig. 18.

Plecanium depravatum Schwager 1865, p. 93, pl. 2, fig. 3.
Textilaria flexa Kubler and Zwingli 1870, p. 35, pl. 4*i*, fig. 17.
Textilaria argoviensis Haeusler 1881, p. 36, pl. 2, figs. 61, 62.
Textilaria scyphiphila Uhlig 1881, p. 136, pl. 15, figs. 2, 3.
Textularia jurassica (Gümbel), Paalzow 1932, p. 94, pl. 4, figs. 21–23.
Textularia racemata (Terquem and Berthelin), Franke 1936, p. 125, pl. 12, fig. 20.
Textularia agglutinans d'Orbigny, Bartenstein and Brand 1937, p. 182, pl. 14*a*, figs. 5*a*, *b*; pl. 14*c*, fig. 16; pl. 15*a*, figs. 40*a–c*; pl. 15*b*, figs. 3*a–c*; pl. 15*c*, figs. 21*a*, *b*.
Textularia jurassica (Gümbel), Seibold and Seibold 1953, p. 43, pl. 4, fig. 2.
Textularia jurassica (Gümbel), Seibold and Seibold 1955, p. 98, text-figs. 2*a*, *b*; pl. 13, fig. 1.

Description. After the first few chambers the margins diverge at an angle between 8° and 18°. The early chambers are wider than high, later chambers sub-globular. All sutures are depressed, the lateral sutures normal to the long axis of the test. The agglutinated material is 5–10 μ pyrite or fine-grained quartz with a calcareous cement. The aperture is sub-circular on the basal suture of the end chamber.

Remarks. Variable characters include the size of the test at which sub-globular chambers first appear, the rapidity of the change to the sub-globular type which may be abrupt or transitional over seven or eight chambers, and the relative position of pairs of chambers with consequent modification of the median suture. Variation in the latter is wide. All intermediates can be found between a form with chambers tending to lie side by side and a median suture of alternate long and short elements, and a form in which successive chambers are nearly superposed and the lateral sutures are shortened so that a cuneiform, uniserial condition is approached.

T. jurassica was common from the *baylei* to *rotunda* zones.

Textularia auensteinensis (Haeusler)

Plate 54, fig. 27

Textilaria auensteinensis Haeusler 1881, p. 40, pl. 2, fig. 72.
Textilaria alsatica Andreae 1884, p. 214, pl. 6, figs. 5*a*, *b*.
Textilaria oxfordiana Deecke 1886, p. 324, pl. 1, fig. 24.

Description. For most of the test the margins diverge at an angle between 10° and 12°. All chambers are twice as wide as high and are never inflated. The sutures are gently depressed, the lateral sutures lie obliquely to the long axis of the test at angles between 50° and 60°. The agglutinated material is fine-grained quartz or pyrite. The aperture is a semicircular opening on the basal suture of the end chamber.

Remarks. Occurs rarely from the *grandis* sub-zone to the *rotunda* zone.

Spiroplectammina biformis (Parker and Jones)

Plate 54, fig. 28

Textularia agglutinans d'Orbigny, var. *biformis* Parker and Jones 1865, p. 370, pl. 15, figs. 23*a*, *b*.
Spiroplectammina biformis (Parker and Jones), Bartenstein and Brand 1937, p. 183, pl. 2*b*, fig. 39.

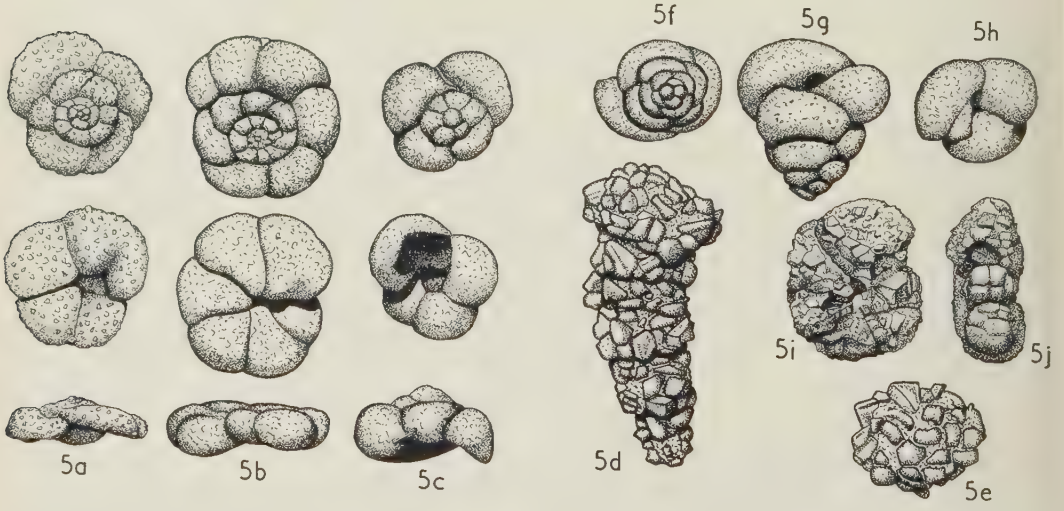
Description. The test consists of an initial evolute coil of six chambers, arranged in a single whorl, followed by a biserial part closely similar to that of *T. jurassica* but with larger chambers. The agglutinated material is pyrite or fine-grained quartz. The aperture is a semicircular opening on the basal suture of the end chamber.

Remarks. It is possible that these forms are microspheres of *T. jurassica*. Occurs frequently in the *wheatleyensis* sub-zone and rarely in the *pectinatus* zone.

Trochammina squamata Jones and Parker

Plate 54, fig. 29; text-fig. 5*a*

Trochammina squammata Jones and Parker 1860, p. 304.
Trochammina squamata Jones and Parker, Paalzow 1932, p. 96, pl. 4, figs. 24–26.
Trochammina squamata Jones and Parker, Bartenstein and Brand 1937, p. 190, pl. 6, fig. 41; pl. 11*b*, fig. 29; pl. 15*c*, figs. 22*a*, *b*.



TEXT-FIG. 5. *Trochammina*, *Reophax*, *Haplophragmoides*, and *Eggerella?* 5*a*, Dorsal, ventral, and lateral views of *Trochammina squamata*, P. 43978, ×41, *baylei* zone, Black Head, near Osmington Mills, Grid ref. 30/727818. 5*b*, Dorsal, ventral, and lateral views of *T.* cf. *nitida*, P. 43979, ×72·5, Crushed Ammonoid Shales, *rotunda* zone, Hounstout, Grid ref. 30/947773. 5*c*, Dorsal, lateral, and ventral views of *T. globigeriniformis*, P. 43980, ×102·5, *pectinatus* zone, Freshwater Steps, Grid ref. 30/942773. 5*d*, *e*, Lateral and terminal views of *Reophax hounstoutensis* sp. nov., holotype, P. 43984, ×36. 5*f*, *g*, *h*, Lateral, initial, and terminal views of *Eggerella? meentzeni*, P. 43981, ×82, *mutabilis* zone, Black Head, near Osmington Mills, Grid ref. 30/727818. 5*i*, *j*, Lateral and peripheral views of *Haplophragmoides haeusleri* sp. nov., holotype, P. 43985, ×43·5.

Description. Test trochospiral. The ventral surface is gently concave with only the four to seven chambers of the last whorl visible. The dorsal side is a low spire with three or four whorls exposed. The sutures are depressed. The agglutinated material is a mixture of fine and medium quartz set in a calcareous cement. The aperture is semicircular, basal on the ventral spiral suture of the end chamber.

Remarks. Occurs frequently from the *baylei* zone to the *mutabilis* zone.

Trochammina cf. *nitida* Brady

Plate 54, fig. 30; text-fig. 5*b*

Cf. *Trochammina nitida* Brady 1881, p. 52, pl. 41, figs. 5, 6.

Description. Test trochospiral, discoidal. The ventral surface is gently convex with the five to seven chambers of the last whorl visible. The dorsal surface may be either gently convex or concave with three or four whorls exposed. The sutures are distinct but little depressed. The agglutinated material is fine-grained quartz or pyrite with a calcareous cement. The aperture is semicircular, ventral on the basal suture of the end chamber.

Remarks. Occurs rarely from the *mutabilis* to *pallasioides* zones.

Trochammina globigeriniformis (Parker and Jones)

Plate 54, fig. 31; text-fig. 5*c*

Lituola nautiloidea Lamarck, var. *globigeriniformis* Parker and Jones 1865, p. 407, pl. 15, figs. 46, 47; pl. 17, figs. 96–98.
Trochammina globigerinoides Haeusler 1882, p. 352, pl. 15, figs. 8, 9.
Trochammina globigerinoides Haeusler 1890, p. 66, pl. 10, figs. 20–22.
Trochammina globigeriniformis (Parker and Jones), Bartenstein and Brand 1937, p. 189, pl. 1*a*, fig. 21; pl. 4, fig. 13; pl. 5, fig. 76.
Trochammina globigeriniformis (Parker and Jones), Seibold and Seibold 1953, p. 46, fig. 5, 2.

Description. Test small, trochospiral. The ventral surface has a deep but narrow umbilicus. The dorsal surface is a well-developed spire with $1\frac{1}{2}$ to $2\frac{1}{2}$ whorls exposed. There are usually four globular chambers in the last whorl, separated by deeply depressed sutures. The agglutinated material is medium or fine quartz or pyrite. The semicircular aperture is basal on the ventral spiral suture.

Remarks. Occurs frequently throughout the Kimeridgian.

Eggerella? meentzeni (Klingler)

Plate 54, fig. 32; text-figs. 5*f–h*

Valvulina meentzeni Klingler 1955, p. 201, pl. 12, figs. 13*a–c*.

Description. Test trochospiral. The globular proloculum is followed by a whorl with 4 to $4\frac{1}{2}$ chambers. Later whorls show a regular reduction in the number of chambers though triserial to biserial or uniserial. There is sometimes an increase in the number of chambers in the last whorl. All chambers are inflated with depressed sutures. The agglutinated material is 10–20 μ quartz with little calcareous cement. The aperture in forms with a polyserial last whorl is semicircular and basal. In the terminally uniserial forms it is circular, central in the apertural face which may be directed at right angles to the axis of coiling.

Remarks. Twenty individuals were found in the *mutabilis* zone and two at the top of the *pectinatus* zone.

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DEVONIAN MEGASPORES FROM ARCTIC CANADA

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ABSTRACT. A megaspore assemblage is described from coal and shale deposits of Upper Devonian age from Ellesmere Island, Arctic Canada. All are new species, and two represent new genera: *Biharisporites ellesmerensis* sp. nov., *B. ocksensis* sp. nov., *Triangulatisporites rootsii* sp. nov., *Lagenicula devonica* sp. nov., *Ocksisporites maclarenii* gen. et sp. nov., and *Nikitinsporites canadensis* gen. et sp. nov. All but one of these forms are appreciably smaller than typical Carboniferous megaspores. There appears to be a general rise in the mean size of megaspores from the Devonian to the Carboniferous, followed by a diminution in size through the Mesozoic. This may be correlated with the corresponding rise and decline of the arborescent lycopods.

INTRODUCTION

THE plant microfossils described in this paper were obtained from some samples of bituminous coal and shale of Upper Devonian age from Ellesmere Island, Arctic Canada. The study has been restricted to those spores greater than 200 μ in diameter. With a few exceptions triradiate spores of this size are generally regarded as megaspores of heterosporous plants. The smaller spores present, not dealt with here, may represent the isospores of homosporous plants, the microspores of heterosporous plants, and possibly even pollen (if true seed plants existed in the Devonian).

The occurrence of megaspores of Devonian age is in itself of significance in suggesting the presence of some abundance of heterosporous plants at this time. In the Carboniferous of the northern hemisphere there is a great diversity of megaspores in suitable facies, and many of these have now been correlated with particular genera, and even species, of arborescent lycopods (Felix 1954; Chaloner 1953*a*, *b*). In this context, a Devonian megaspore assemblage has particular significance for comparison with the earliest known Carboniferous megaspores.

I am pleased to express my thanks to Dr. Wayne Fry, to Dr. Colin McGregor of the Canadian Geological Survey and also to the Director of that Survey for making this material available to me.

Source and age of the material. The three specimens from which megaspores were obtained were all collected from Ockse Bay, on the south-west coast of Ellesmere Island. One sample, 4713, was collected from a coal seam at the head of Ockse Bay by E. F. Roots (Canadian Geological Survey Plant Type Locality 13001). The other two samples, collected by D. J. Mclaren, are a sandy shale (sample 4747) from the Ockse Bay section (Plant Type Locality 13003), and a bituminous coal (sample 4742) from the mud-flat talus on the eastern arm of Ockse Bay (Plant Type Locality 13002). The coal of sample 4713, occurring *in situ*, is Upper Devonian, and the spore contents of coal 4742 from the talus is consistent with its having come from the same horizon. According to Dr. Wayne Fry (personal communication) the section from which the samples (4713 and 4747) came 'overlies transitionally beds of known Middle Devonian age, based on a marine fauna; the flora of the upper beds is that described by Nathorst (1904) . . .'.

Methods of spore preparation. The coal samples were macerated for several days in

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Schulze's solution (concentrated nitric acid and potassium chlorate). The residue was then washed and dilute alkali was added. This was decanted off after several hours and replaced by water, and this too was decanted off. Washing and decanting were repeated several times, the residue being allowed to settle out completely each time. The final residue was examined under a binocular microscope and the larger spores picked out with a pipette. Some of the spores were allowed to dry, and mounted as opaque objects (cf. Pl. 55, fig. 7). Others were placed in concentrated nitric acid until transparent, and then transferred to distilled water; these were mounted in glycerine jelly, or dehydrated and mounted in balsam for examination by transmitted light (cf. Pl. 55, fig. 1).

The shale was treated with cold dilute hydrofluoric acid in a polythene beaker for several days. The residue (which still contained quite a lot of undissolved mineral matter) was washed several times by adding water and decanting, and the larger spores were then picked out of the residue as with the coal macerations.

Taxonomy of Palaeozoic megaspores. Prior to 1954 nearly all Palaeozoic megaspores (i.e. spores of more than 200 μ diameter) were placed in a single genus, *Triletes*. Most palaeobotanists accepted this as a genus consisting principally of the megaspores of the heterosporous lycopods. Correlation of a few of these megaspores with their parent plants established that the spores of at least a number of different genera were included in *Triletes* (Schopf, Wilson, and Bentall 1944).

In 1954 Potonié and Kremp published a revision of Palaeozoic spore genera, which they later amplified (1955, 1956*a*, 1956*b*). This revision recognized thirteen genera in place of the old genus *Triletes*, which they rejected completely as a confused name. The basis of their treatment was spore morphology, without regard for the natural relationships of those spores of which the parent plants were known. While this resulted in a seemingly clear-cut definition of genera, some were manifestly very artificial. The spores known to have been borne by *Sigillaria*, for example, a well-circumscribed group (Chaloner 1953*b*), were separated into two genera on features of wall decoration. In a later work Potonié (1958) erected further genera on the basis of species included by other authors in *Triletes*. Many of the diagnostic characters which he uses are of an order which earlier workers had regarded as being only of specific value.

Some splitting of the genus *Triletes* was clearly desirable, but this increasing multiplicity of megaspore genera has had several disadvantages. Firstly, as already indicated, it cuts across known biological relationships; secondly, it gives an exaggerated impression of the degree of difference between different assemblages; and finally, the generic limits become so finely drawn that almost every new species requires a new genus to accommodate it.

I have not attempted to arrange the spores described here into any supra-generic categories. Where nothing certain is known of the parent plants of the spores concerned, such groups may be misleading in implying affinity of their members, where none is known to exist.

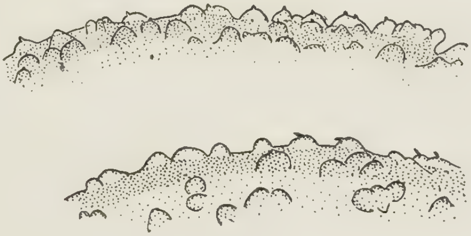
SYSTEMATIC DESCRIPTIONS

Biharisporites ellesmerensis sp. nov.

Plate 55, fig. 2; text-fig. 1

Diagnosis. Triradiate megaspore, circular in the flattened state, with contact faces occupying most of the proximal face of the spore. Greatest diameter 204–304 μ, mean of sixty-four specimens 270 μ. Spore wall apparently of a single layer, covered except on the contact faces with hemispherical to conical warts (coni), typically 7 μ high and 10 μ wide at the base, occasionally having a minute papilla or spine extending from the tip (text-fig. 1). Contact faces lacking warts, bounded by ill-defined arcuate ridges formed by fusion of the warts in that region. Triradiate ridges typically 12 μ wide and rising from about 10 μ in height at their extremities to 25 μ at the pole.

Holotype. The specimen of Pl. 55, fig. 2; slide 4742*a*, Canadian Geological Survey, Ottawa. From sample 4742, a piece of bituminous coal from the mud-flat talus, east arm of Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13002; Upper Devonian.



TEXT-FIG. 1. Decoration of the spore wall of the holotype of *Biharisporites ellesmerensis* sp. nov. ×500, seen in profile at the spore margin. Camera lucida drawing of a transparent preparation. (Slide 4742*a*.)

Discussion. This was the most abundant megaspore present in the two coal samples from Ockse Bay (4742, 4713).

Potonié (1956) recognizes three genera of megaspores having a warty or apiculate decoration, in which this species might be placed: *Tuberculatisporites*, *Verrutriletes*, and *Biharisporites*. Some species of *Tuberculatisporites* obtained from Carboniferous coals are known to be the megaspores of *Sigillaria* (Chaloner 1953*b*). These species have in common a characteristic concavo-convex shape, associated with the peculiar structure of the parent sporangium. It seems desirable to restrict the genus *Tuberculatisporites* to megaspores having this shape, and to exclude from it spores (such as *B. ellesmerensis* sp. nov.) with similar decoration, which were originally more or less spherical.

Potonié (1956) characterizes *Verrutriletes* as having a verrucose decoration of the spore wall, while *Biharisporites* includes similar megaspores with a decoration of uniform coni. The distinction between these two types of decoration depends on the regularity of size and shape of the projections of the spore wall; coni are of uniform size and shape on any one spore, while verrucae are irregular. Clearly, these conditions grade into each other. The projections forming the decoration on these Ellesmere spores approximate to coni in Potonié's sense, and on this basis I include these spores in the genus *Biharisporites*.

The only species of *Biharisporites* recognized by Potonié which is in any sense closely comparable with *B. ellesmerensis* sp. nov., is the Rhaetic *B. myrmecodes* (Harris) Potonié. The Ellesmere spores are about half the diameter of this Rhaetic species, and also differ from it in having the contact faces free of decoration.

While it may seem unwise to include a Devonian spore in a genus based on Gondwanan material, I believe that this is preferable to making a new genus on the basis of very trivial morphological differences. It is inherent in a morphographic system that spores which in all probability are not closely related may be placed in one genus. This is particularly so for spores of a simple, generalized type such as *Biharisporites*. Clearly, other spore genera based on more distinctive or peculiar features (e.g. *Pyrobolospora* Hughes) may represent more natural groups.

Biharisporites ocksensis sp. nov.

Plate 55, figs. 6–8

Diagnosis. Triradiate megaspore, more or less circular in the equatorial plane, 560–1,610 μ diameter, mean of twenty-four spores 925 μ. Spore originally more or less spherical. Triradiate ridges and arcuate ridges slightly elevated; triradiate ridges seven-tenths to nine-tenths of the spore radius. Spore wall up to 40 μ thick; surface finely granular, or covered with minute rounded-conical projections (coni) up to 10 μ high and of about the same width at the base. Decoration uniform over the entire spore surface.

Cotypes. The spores of Pl. 55, figs. 6 and 7; slides 4713*z* and 4713*v* respectively, Canadian Geological Survey, Ottawa. From sample 4713, from a coal seam at the head of Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13001; Upper Devonian.

Discussion. This is the largest of the spore types from Ellesmere, and is comparable in size with some of the large Carboniferous megaspores. The decoration of the wall varies from a fine granular structure (Pl. 62, fig. 7) to minute but well-defined coni visible in profile at the spore margin (Pl. 62, fig. 8). These spores are very similar to some of the large triradiate megaspores of the Lower Carboniferous with a finely granular decoration (cf. *Triletes globuliferus* Dijkstra 1956, *T. subfulgens* Dijkstra); *B. ocksensis* differs from these forms mainly in the character of the wall decoration. It is this feature which excludes it from the several genera of completely smooth-walled megaspores, and I accordingly place it in *Biharisporites* which is characterized by a decoration of small coni. Megaspores of this general type with granular or minutely apiculate walls occur at many horizons from the Devonian onwards.

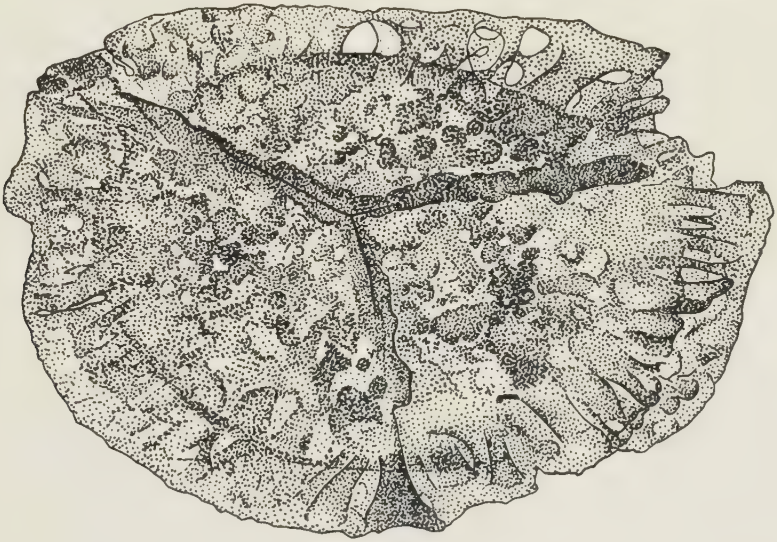
Biharisporites ocksensis differs from previously described species in its relatively large size, and in the dimensions of the coni forming the wall decoration.

Triangulatisporites rootsii sp. nov.

Plate 55, fig. 4; text-fig. 2

Diagnosis. Triradiate megaspore, rounded triangular as seen in an equatorially flattened specimen. Equatorial flange (cingulum) formed of partially fused radiating elements between which gaps occur locally. Diameter, including the flange, measured from one apex of the triangle to the mid-point of the opposite side, 485–524 μ; mean of four specimens 506 μ. Diameter of the spore body 300–370 μ; flange varying in width from 70 μ between the triradiate ridges to 107 μ at the angles. The radiating bars prominent in the flange merge rapidly into a very irregular verrucose to reticulate decoration on the proximal and distal faces.

Holotype. The specimen of Pl. 55, fig. 4; slide 4713*f*, Canadian Geological Survey, Ottawa. From sample 4713, a coal seam at the head of Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13001; Upper Devonian.



TEXT-FIG. 2. *Triangulatisporites rootsii* sp. nov., ×200. Camera lucida drawing of a transparent preparation showing the structure of the flange and decoration of the contact faces. (Slide 4742*d*.)

Discussion. Potonié (1956) recognizes three genera of megaspores with prominent zonal flanges, to which this spore might be referred: *Zonalesporites*, *Superbisporites*, and *Triangulatisporites*. All three are based on Carboniferous holotypes. The first two genera include large megaspores (over 1 mm.) with broad, rather fragile equatorial flanges apparently formed of fused radiating elements. *Triangulatisporites* includes triangular megaspores which are about half this size, and which have a more compact flange, apparently continuous in structure with the spore wall. The flange on this type of spore will not readily break away from the spore body, in contrast to the flange in *Zonalesporites* and *Superbisporites*, which is relatively easily detached.

I include *Triangulatisporites rootsii* sp. nov. in this genus on account of its small size, triangular outline, and the structural continuity of the flange with the spore body wall. This involves a small extension of the limits of the genus both in morphology and in time, but I regard this as preferable to making a new genus at this stage.

Lagenicula devonica sp. nov.

Plate 55, fig. 3

Diagnosis. Triradiate megaspore, with greatly elevated triradiate lips forming an apical prominence. Spore diameter at the equator 270–400 μ, mean of twenty-six spores 337 μ. Height of the spore (measured along the axis) 290–460 μ, mean of fourteen spores 382 μ. Height of the apical prominence alone, from the arcuate ridges to the apex, 97–230 μ, mean of fourteen spores 174 μ. Arcuate ridges prominent, clearly visible in the flattened spore profile. Body of the spore decorated with irregular, more or less conical projections, partially fused to form a verrucose to irregularly reticulate pattern. Apical prominence free of this decoration, but having striate markings or minute corrugations parallel with the spore axis.

Holotype. The spore of Pl. 55, fig. 3; slide 4713*r*, Canadian Geological Survey, Ottawa. From sample 4713, from a coal seam at the head of Ockse Bay, Ellesmere Island. Canadian Geological Survey Plant Type Locality 13001; Upper Devonian.

Discussion. This spore resembles a number of large Carboniferous megaspores with an apical prominence, which are included in the genus *Lagenicula*, e.g. *L. agnina* Zerndt, *L. angulata* Zerndt. It differs from both these species in being less than half their size, and in the very distinctive decoration. The large apical prominence of *Lagenicula devonica* evidently gave the spore a tendency to fall on its side, as with the Carboniferous species. Pl. 55, fig. 3 shows it flattened in this orientation.

Some of the Carboniferous *Lagenicula* species are known to be the megaspores of *Lepidodendron* (Chaloner 1953*a*). It is unlikely that this was the case for *Lagenicula devonica*, but I do not regard this supposition alone as sufficient reason for excluding this spore from the genus *Lagenicula*, with which it agrees in its morphology. This is the only logical way in which a morphographic classification can be applied.

OCKSISPORITES gen. nov.

Type species *O. maclarenii* sp. nov.

Diagnosis. Triradiate megaspore with a broad equatorial flange, having a sharply defined triangular outline. Cavity of the flattened spore circular, diameter less than half the greatest dimension of the whole spore. Flange margin coarsely serrate.

Ocksisporites maclarenii sp. nov.

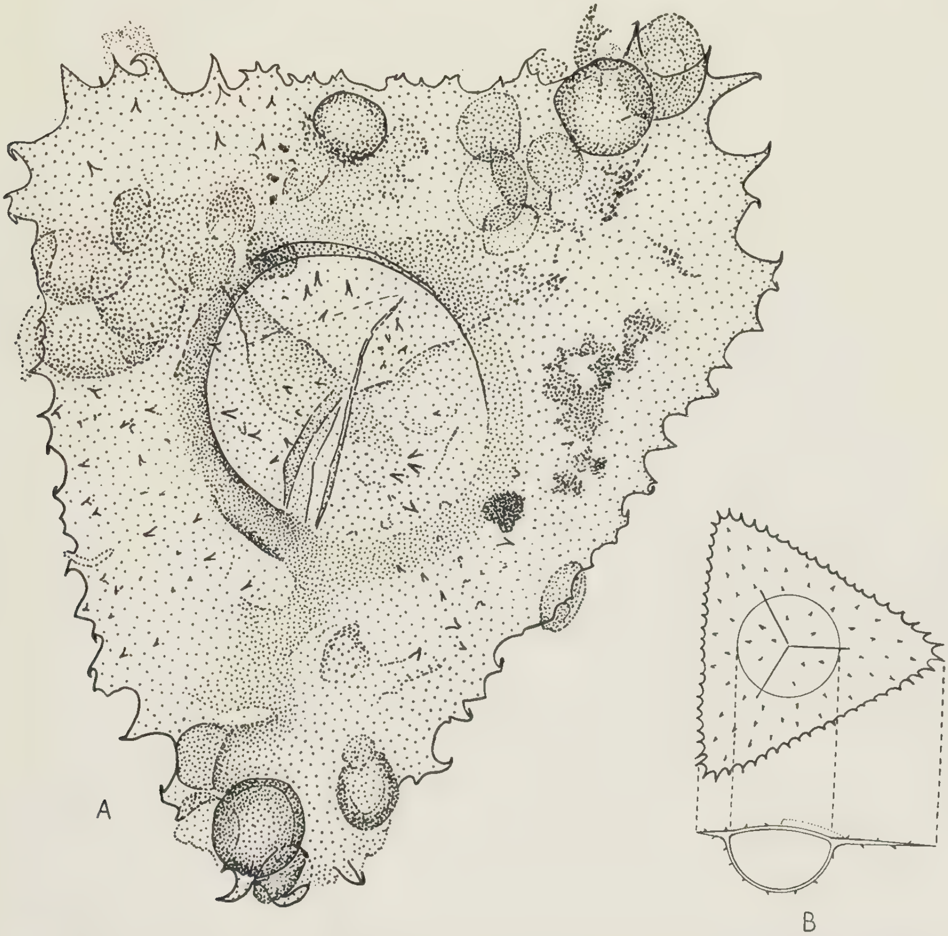
Plate 55, fig. 1; text-fig. 3

Diagnosis. Triradiate megaspore, with a continuous equatorial flange, broadest opposite the triradiate ridges, giving the spore a sharply triangular outline. Sides of the triangle straight to slightly convex. Greatest dimension of flattened spore, from apex of triangle to mid-point of opposite side, 440–630 μ, mean of eight spores 560 μ. Cavity of the flattened spore circular, diameter 240–290 μ, mean of six specimens 260 μ. Width of flange typically 150 μ opposite the triradiate ridges, and 100 μ between them. Triradiate ridges extending to the margin of the spore cavity and sometimes onto the flange; up to 170 μ long and 30 μ high at the pole, diminishing in height towards the margin. Margin of the flange serrate, with sharply pointed teeth typically 20 μ, occasionally up to 60 μ long. Both surfaces of the spore, including the flange, covered with minute spines with swollen bases and sharply drawn-out apices; typically 10 μ long, but smaller on the proximal face over the area of the spore cavity. No arcuate ridges present.

Holotype. The specimen of Pl. 55, fig. 1; slide 4742*e*, Canadian Geological Survey, Ottawa. From sample 4742, a piece of coal from the mud-flat talus, eastern arm of

Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13002; Upper Devonian. This spore was also obtained from samples 4713 and 4747 from the same vicinity.

Discussion. A hypothetical reconstruction of this spore is shown in text-fig. 3B. It can be seen that the thickest part of the flattened spore is around the margin of the spore cavity. This part accordingly appears darkest in the transparent preparations (Pl. 55, fig. 1). I attribute this thickness to the vertical compression of the equatorial part of the spore wall, where the flange joins the spore.



TEXT-FIG. 3. *A. Ocksisporites maclarenii* gen. et sp. nov., ×200. Camera lucida drawing of a transparent preparation; some small spores are shown adhering to the megaspore. (Slide 4742*g*.) *B.* Diagrammatic reconstruction ×50, in plan and median section.

O. maclarenii differs from previously described megaspores in the relatively large continuous flange with a serrate margin, which gives the spore its sharply triangular outline.

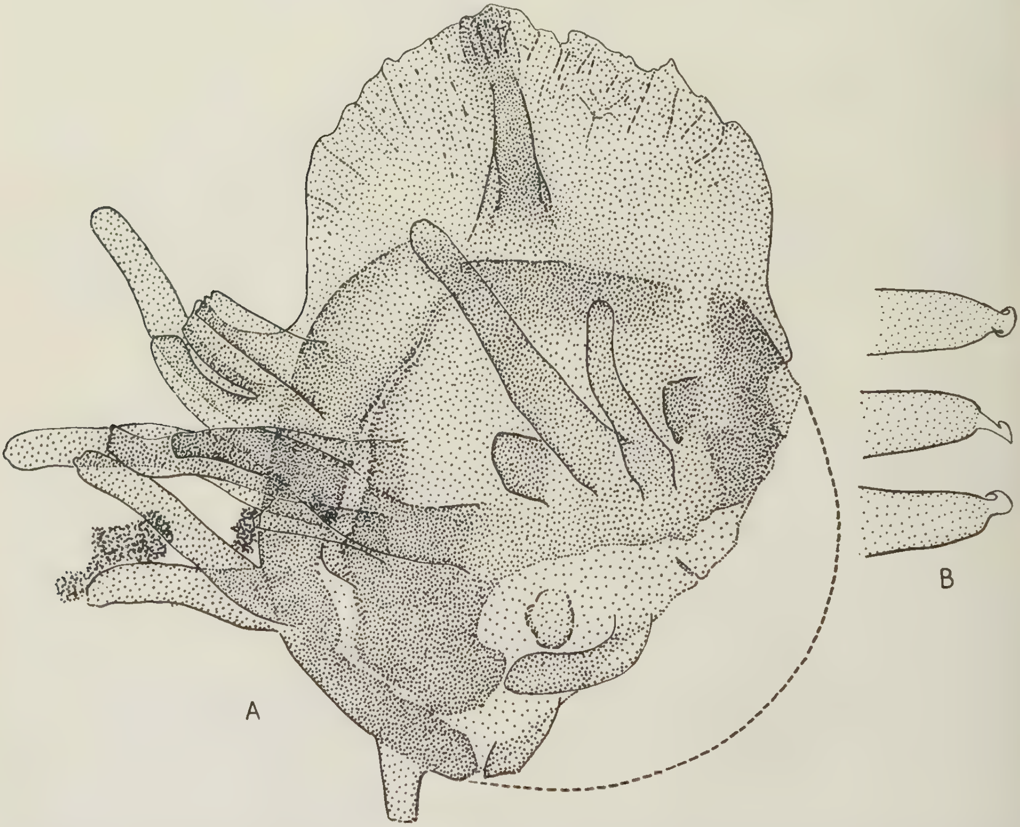
NIKITINSPORITES gen. nov.

Type species *N. canadensis* sp. nov.

Diagnosis. Megaspore with greatly elevated triradiate lips forming an apical prominence; spore body, except for the lips, covered with thick spines, parallel sided for most of their length, tapering sharply at the apex to end in an anchor-shaped bifurcation.

Nikitinsporites canadensis sp. nov.

Plate 55, fig. 5; text-fig. 4



TEXT-FIG. 4. *A*. *Nikitinsporites canadensis* gen. et sp. nov., ×200. Camera lucida drawing of a transparent preparation of one of the cotypes. The apical prominence is uppermost; the anchor-shaped spine apices are missing. The dotted line shows the outline of the missing part of the body of the spore. *B*. Anchor-shaped spine apices from another specimen, ×400. (Slides 4713*ac* and 4713*ab* respectively.)

Diagnosis. Triradiate megaspore, body more or less circular when flattened, 390–610 μ diameter, mean of eleven specimens 525 μ. Triradiate lips greatly expanded to form an apical prominence, up to 195 μ high, mean of eleven specimens 140 μ. Height of spore, including the apical prominence, 390–710 μ, mean of ten specimens 573 μ. Spore wall, excluding the triradiate lips and contact faces, covered with thick spines typically 200 μ long and 30 μ diameter. Spines tapering very gradually from the base, contracting rapidly at the apex to a bifurcated anchor-shaped tip. Width of this anchor-shaped apex always less than that of the main part of the spine. Spore wall typically 25 μ thick, up to 40 μ in the largest spores.

Cotypes. The specimens of Pl. 55, fig. 5 and text-fig. 4A, both on slide 4713*ac*, Canadian Geological Survey, Ottawa. From sample 4713, from a coal seam at the head of Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13001; Upper Devonian.

Discussion. The anchor-shaped apices of the spines on these spores are evidently very fragile, and are missing from many of the spines. Usually, when this is the case, a small papilla is left at the apex of the relatively thick spine (text-fig. 4A and B). These spores are clearly very similar to those described by Nikitin (1934) occurring in sporangia of Upper Devonian age, to which he gave the name *Kryshtofovichia africani*. The megaspores of *Kryshtofovichia* have an even taller apical prominence than those described here, but in all other respects are closely similar. Nikitin's name, *Kryshtofovichia africani*, is based on both mega- and microsporangia, which he believed with good reason to have belonged to the same plant. This name could not therefore be used for isolated megaspores, however similar to those in the sporangia (see discussion in Schopf and others 1944, p. 21). I regard the genus *Nikitinsporites* as including spores of the type contained in *Kryshtofovichia africani*, if found isolated.

A much smaller spore than those just described, but having a triradiate symmetry and anchor-shaped spine apices has long been known from the Devonian under the name 'Lang's Type G'. This was first described by Lang (1925) from the Middle Old Red Sandstone of Scotland. This type of spore was subsequently described from a number of other localities in rocks of similar age (Kräusel and Weyland 1929, Middle Devonian of Elberfeld; Arnold, 1936, Upper Devonian of Scaumenac, Canada and Pittston, Pa., U.S.A.; Høeg 1942, Middle Devonian of Spitzbergen; Hoffmeister and others 1955, Middle Devonian of Alberta; I have also obtained them from the Upper Devonian of Perry, Maine, U.S.A.). Eisenack 1944, described new material of Lang's Type G and gave it the name *Triletes ancyreus*. His material differed from that described by the other authors in having elevated triradiate lips forming an apical prominence, and he figured spores flattened laterally to show this feature.

Finally, Naumova (1953) described various triradiate spores with anchor-shaped spines, some similar to Lang's Type G, under the generic name *Archaeotriletes*. Potonié (1958) has emended this genus, and validated it by citing a type species and a holotype.

There is now evidently partial synonymy between 'Lang's Type G', certain of Naumova's *Archaeotriletes* species, and *Triletes ancyreus* Eisenack. The spore described here as *Nikitinsporites canadensis* differs from all of them in its much greater size, its very thick scarcely tapering spines and the large apical prominence. I have accordingly preferred to make a new genus, *Nikitinsporites*, rather than to include this spore as a species of *Archaeotriletes*.

GENERAL DISCUSSION

Origin of the spores. There are several groups of heterosporous plants in the Upper Devonian flora which could have produced the megaspores described here. The more important are the lycopods and the heterosporous ferns (cf. *Archaeopteris*). However, it is possible that other groups, including even non-vascular plants, might be represented. At least one plant, believed to be of a non-vascular nature, produced large (*c.* 200 μ) resistant spores with a triradiate mark (Kidston and Lang 1924; Arnold 1954). Any generalization concerning parent plants of the Ellesmere megaspores must therefore be very tentative.

Two of the six species described here show some similarity with Carboniferous megaspores which have been attributed to the lycopods (*Triangulatisporites* and *Lagenicula*). While such a correlation cannot be reliably extended, even at a generic level, beyond the species for which it was established, such similarity offers at least a suggestion of relationship. Nikitin (1934) believed that his *Kryshtofovichia africani* was a lycopod. If he was right, this implies a similar origin for the *Nikitinsporites* megaspores described here.

Spores similar to Lang's Type G have been recorded in close association with *Aneurophyton* (Kräusel and Weyland 1929), but there is no conclusive evidence that they actually represent the spores of this plant. In view of their widespread occurrence in the upper part of the Devonian, a correlation with their parent plant would be particularly interesting.

Comparison with other megaspore assemblages. Sen (1958) has recently redescribed and figured some megaspore casts from the Upper Devonian of Bear Island, originally figured by Nathorst. They are remarkable in being far larger than any other Devonian forms known (including those described here), and in this and other respects resemble Carboniferous ones. Sen identifies one spore from the Bear Island assemblage with a species previously known only from the Upper Carboniferous. As there is no reason to doubt the age of the Bear Island material, the similarity of these spores to Carboniferous forms is disconcerting. The apparent anomaly presented by Sen's results emphasizes the need for further work on Devonian megaspores.

If the various assemblages of megaspores from different horizons are compared on the basis of size alone, those from the Carboniferous are by far the largest (excluding the Bear Island material just mentioned). As Dijkstra (1949, p. 30) has pointed out, Mesozoic megaspores are distinguishable from Carboniferous ones, taken collectively, simply on the basis of their much smaller size, without regard to their morphology. This

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EXPLANATION OF PLATE 55

The photograph of fig. 7 was taken by reflected light, the remainder by transmitted light. Fig. 8 is ×800, the remainder are all ×100.

Figs. 1–8. Megaspores from the Upper Devonian of Ockse Bay, Ellesmere Island.

Fig. 1. *Ocksisporites maclarenii* gen. et sp. nov., holotype. From sample 4742, slide 4742*e*.

Fig. 2. *Biharisporites ellesmerensis* sp. nov., holotype. From sample 4742, slide 4742*a*.

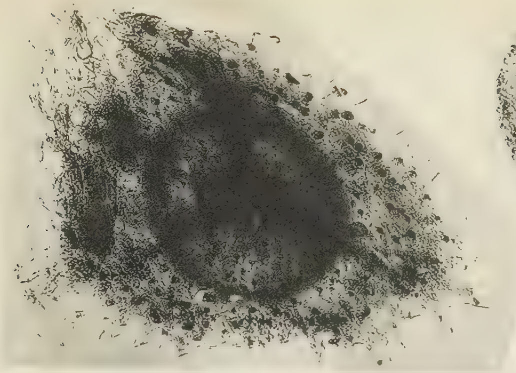
Fig. 3. *Lagenicula devonica* sp. nov., holotype. From sample 4713, slide 4713*r*. The apical prominence is uppermost, and the arcuate ridges lie more or less across the centre of the flattened spore; one of the triradiate ridges is slightly to the right of the centre.

Fig. 4. *Triangulatisporites rootsii* sp. nov., holotype. From sample 4713, slide 4713*f*.

Fig. 5. *Nikitinsporites canadensis* gen. et sp. nov., Cotype. From sample 4713, slide 4713*ac*.

Figs. 6–8. *Biharisporites ocksensis* sp. nov. 6, 7, Cotypes; sample 4713, slides 4713*z*, and 4713*v* respectively. 8, Part of the spore margin, showing the decoration in profile.

All the slides are in the Canadian Geological Survey, Ottawa, Canada.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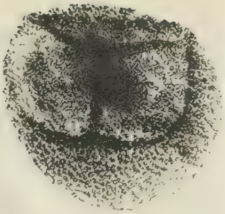
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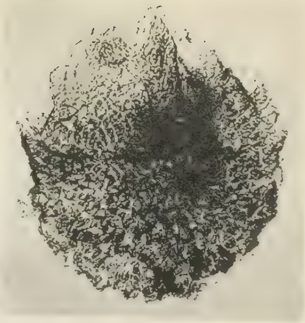
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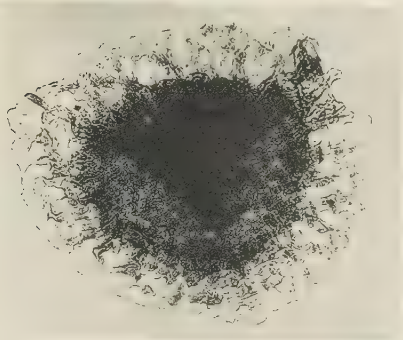
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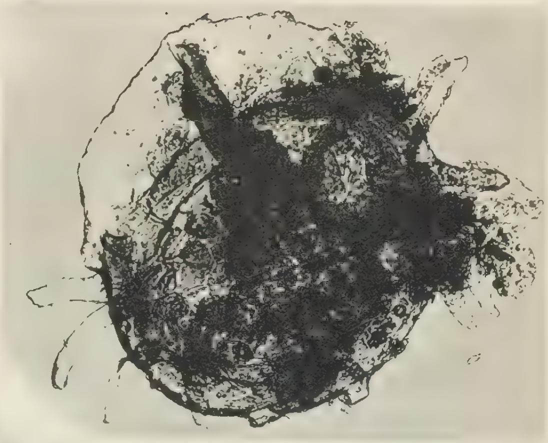
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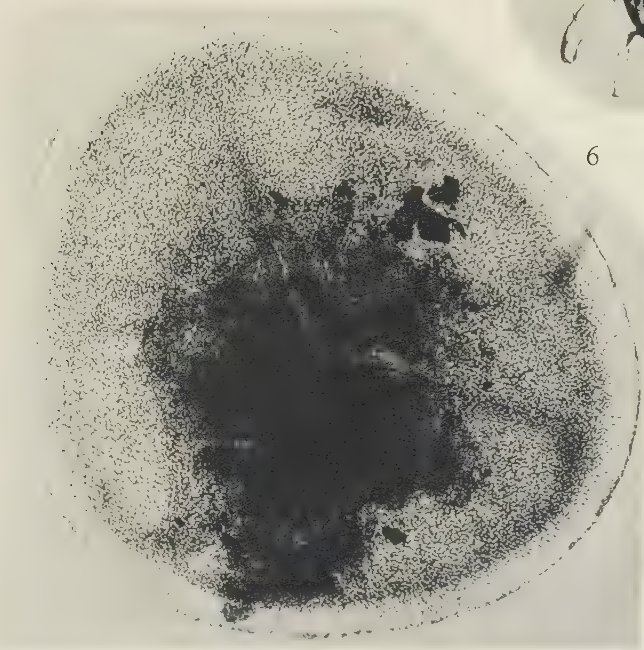
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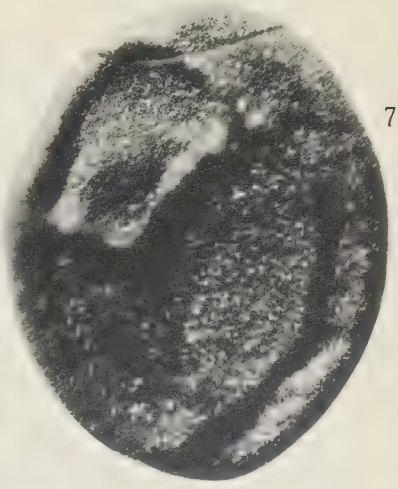
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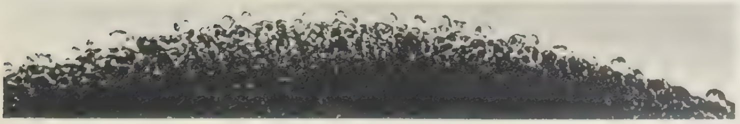
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CHALONER, Devonian megaspores

general trend of size decrease can be seen from Table 1. Obviously these data depend on a whole series of subjective and other extraneous factors (e.g. the limits that are placed on species) and new discoveries may completely alter this picture.

TABLE 1

Age	*Number of species*	*Mean spore diameter for all species*
Upper Cretaceous (Dijkstra 1949) . .	13	402 μ
Lower Cretaceous (Dijkstra 1951) . .	26	431 μ
Middle Jurassic (Kendall 1942; Murray 1939)	7	421 μ
Rhaetic (Harris 1935)	14	603 μ
Permian (Surange and others 1953) . .	18	685 μ
Carboniferous (Dijkstra 1946) . . .	34	1,600 μ

Table 1. Showing the mean size for all the species, taken collectively, of each of several megaspore assemblages. The second column gives the number of species recognized in each assemblage. The figures show a general decrease in the mean size of the megaspores from the Carboniferous to the Cretaceous.

Most of the large Carboniferous megaspores are known to have been borne by arborescent lycopods (Felix 1954; Chaloner 1958*a*) which were one of the main elements in the coal swamp vegetation. It is significant that two of the smallest Carboniferous megaspores were apparently borne by herbaceous lycopods (Chaloner 1954, 1958*b*). Such evidence as is available from the macrofossils suggests that most Mesozoic lycopods, in contrast to the Carboniferous ones, were at least small, if not entirely herbaceous types. It is therefore a plausible hypothesis (accepting the provisos made above) that the decline in megaspore size shown in Table 1 may be correlated with the decline in the arborescent lycopods, as distinct from the herbaceous ones.

The megaspores described here, as with most of the larger spores recorded from the Devonian (Lang, Høeg, loc. cit.) are far smaller than the Carboniferous ones. On size alone the Ellesmere megaspore assemblage looks much more like a Mesozoic than a Carboniferous or Permian one. It may be that they represent, at least in part, the herbaceous lycopod stock which was later to continue side by side with the arborescent forms so prominent in the Carboniferous, and which ultimately survived them into the Mesozoic.

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THE *MARTINIOPSIS*-LIKE SPIRIFERIDS OF THE QUEENSLAND PERMIAN

by K. S. W. CAMPBELL

ABSTRACT. The three brachiopod genera *Martiniopsis* Waagen, *Notospirifer* Harrington, and *Ingelarella* nov. are included in the new subfamily Ingelarellinae of the family Spiriferidae. The detailed morphology of the group is discussed, *Notospirifer* is redefined, and *Ingelarella* and its type species are described. It is concluded that *Martiniopsis* is restricted to the Tethyan–Ural area, while *Notospirifer* is as yet recorded only from Australia, and *Ingelarella* occurs in Australasia, Argentina, and possibly Pakistan and Kashmir. All three genera appear to be restricted to the Permian (Sakmarian–Tartarian).

INTRODUCTION

SINCE the work of Etheridge (1892) no critical work has been done on the spiriferid brachiopods from the Queensland Permian which are commonly placed in *Martiniopsis* Waagen. It has been customary to refer all specimens to *M. subradiata* (Sowerby) and its sub-species, *M. darwini* (Morris) or *M. oviformis* (M'Coy). Representatives of the group are found throughout the marine Permian deposits of the State, often in great abundance, and they exhibit a very wide range of variation. There are two genera involved—*Notospirifer* Harrington and *Ingelarella* nov.—which together are represented by some twenty-three species. The species all have a fairly restricted stratigraphic range, and it has been found possible to use them for correlation on both a regional and inter-basinal scale. No forms referable to *Martiniopsis* Waagen have yet been discovered, and it now appears that that genus was restricted to the warmer waters of the Tethyan–Ural region, while *Notospirifer* and *Ingelarella* characterize the cooler water Gondwana province.

Family SPIRIFERIDAE King 1846

Subfamily INGELARELLINAE nov.

Diagnosis. Spiriferidae of very variable size; hinge line variable in length but always less than the maximum width of the shell; cardinal extremities rounded; fold and sinus present or absent; commissure rectimarginate to parasulcate and sulciplicate; cardinal areas invariably present on each valve; delthyrium partly obstructed by narrow dental ridges; lateral slopes smooth or bearing up to six deep rounded plications; shell substance in two layers—a very thin 'epidermoidal' layer and a thick inner fibrous layer; outer layer bearing shallow pits of variable shape; teeth supported on well-developed dental lamellae; ventral adminicula diverge at variable angles; dorsal adminicula range in length from one-third the length of the valve to absent; crural plates strong; spires with from about twelve to twenty-five volutions; no jugum present.

Remarks. This subfamily is erected to include *Martiniopsis* Waagen, *Notospirifer* Harrington and *Ingelarella* gen. nov. I have erected it on *Ingelarella* gen. nov. in preference to *Martiniopsis* Waagen or *Notospirifer* Harrington, because the former genus is much more adequately known, and because of the inaccessibility of type material of *Martiniopsis*,

[Palaeontology, Vol. 1, Part 4, 1959, pp. 333–50, pls. 50–57.]

and my inability to locate the type locality of *Notospirifer darwini* (Morris), the type species of *Notospirifer*. In his original work Waagen placed the genus *Martiniopsis* in the subfamily Martiniinae (Waagen 1883), and most subsequent authors have acquiesced in this assignment (Schuchert and Le Vene 1929; Douglas 1940). Tschernyschew, however, put it in the Delthyrinae. The apparent similarity of *Martinia* and *Martiniopsis* is, however, due to homeomorphy and there is little similarity between *Martinia* and the other genera here included in the Ingelarellinae. Fredericks (1926), basing his subfamilies primarily upon the internal structure of the pedicle valve, separated *Martiniopsis* from *Martinia* and placed it in the section 'glabratae-levis' of his subfamily Munellinae in which apical plates are developed. The artificiality of this classification has been pointed out by several authors (George 1933; Maxwell 1954), and most workers find it quite unacceptable except as a classificatory key.

In the opinion of Harrington (1955), *Notospirifer* is a member of the Phricodothyrinae Caster, but this assignment is the result of a misconception of the nature of the ornament of his genus. As is shown hereunder, *Notospirifer* bears a superficial ornament of surface pits, and not spines as do the phricodothyrinids; and further, it does not have the reticulate shell structure of that group.

Australian authors dealing with the so-called *Martiniopsis* of eastern Australia have never classified them under a subfamily.

SHELL STRUCTURE

Of the shell structure of *Martiniopsis*, Waagen (1883, p. 524) reported: 'The shell is coated with an epidermis which exhibits a very distinct punctation, very similar to the punctation of *Terebratula*. The median shell layers show this punctation much less distinctly, though it can be well observed in places. The punctation is very fine, close, and arranged in quincunx.' Opposed to this is the conclusion of Browne (1953, p. 103) that the Salt Range specimens which she examined were impunctate, and that the so-called punctation is no more than a delicate surface ornament.

Morris (1845, p. 281) was the first to remark on the punctation of Australian specimens, and he apparently appreciated the fact that it was a superficial phenomenon—'the surface of the shell marked by numerous, minute, elongated punctations . . .'. de Koninck (1877, p. 178 English translation) considered that the surface of forms referred by him to *Spirifer darwini* was covered with granulations rather than punctations, but this was apparently the result of faulty observation. The same author relegated certain Ingelarellinids to *Spirifer glaber*, but noted that the test was thin and perforated, and that 'the whole surface is covered with well marked punctures arranged quincuncially'.

Etheridge observed the shell structure of Ingelarellinids from numerous localities in eastern Australia, presenting his conclusions in two works (1892, pp. 238–9; 1919, p. 185), but it would appear that he was never certain of the intimate structural details. Of some Queensland specimens he states: 'Wherever the surface is abraded this striation has the appearance of longitudinal tubes running through the substance of the test; but on those portions merely smoothed over by the denuding agent, these tubes appear as darker lines traversing the lighter coloured limestone of which the shell is composed' (1892, p. 239). It is difficult to conclude from this whether he believed the 'tubes' in question to be punctae or not. After an examination of specimens from the New South Wales South Coast he reported that: 'It would appear as if some layers of the test were fibrous, others punctate, hence I used the term "punctate-fibrous"' (1919, p. 185). However, in well-preserved specimens from the Upper Marine of the Hunter Valley 'there is visible on the exteriors a remarkably delicate and fine, longitudinal, tear-like sculpture, which may be of an epidermal nature, but it is not accompanied by perforations, so far as I can see'.

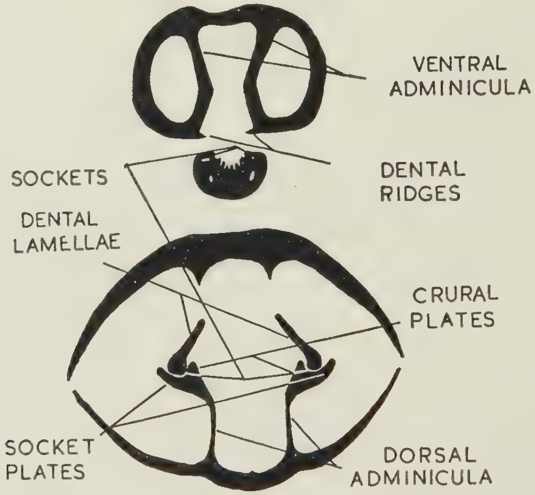
In this study I have examined thin sections of the shells of several species of both *Ingelarella* and *Notospirifer* and have reached the following conclusions: (1) In both *Ingelarella* and *Notospirifer* the wall is composed of two distinct layers, a thin outer layer and a thick inner fibrous lamellar layer, often referred to as the primary and secondary layers (cf. Williams 1956). (2) The outer layer is much thicker in *Notospirifer* than *Ingelarella*. This layer (the epidermis of Waagen and Etheridge) carries quincuncially arranged pits, and this therefore accounts for the difference in the depth of the pits in the above genera. It covers the whole outer surface of the valves. The fibres of which it is composed are very fine (usually visible only at magnifications above 50), and are arranged with their length approximately at right angles to the surface of the shell. (3) The inner layer is formed of layers of fibres which in longitudinal section are inclined obliquely forward from the outside to the inside of the shell. Within each layer the fibres are subparallel, but they are highly irregular in direction. At any position in the shell the fibres within neighbouring layers run in different directions. (4) No endopunctae are present.

In a thin section of an undescribed species of *Ingelarella* from Homevale, several small spicular structures composed of structureless calcium carbonate have been observed to run obliquely across the lamellae. The fibres in which they are embedded are arched around them. They are few in number and are irregularly distributed, and certainly are not of sufficient size or abundance to warrant comparison with the pseudo-punctate type of shell structure found in such groups as the stropheodontids. Thin sections of other species have failed to reveal further examples, but specimens of another species from near Theodore show fairly numerous irregular pits in decorticated specimens, which may indicate the presence of spicules. Unfortunately several attempts to prepare thin sections of this material have proved unsuccessful. Specimens of the type species from Mt. Coma (see Pl. 57, fig. 5*a*) show evidence of the projecting ends of these spicular structures in internal moulds.

Surface pits. Surface depressions, which vary in shape from circular pits to linear furrows, and which are restricted to the outer (prismatic) layer of the shell, are found in all members of the subfamily. These structures fall within the definition of Schuchert and Cooper's *exopunctae*. Williams (1956, p. 250) has pointed out that this term has been used to cover several structures of different origin, and hence it has not been used in this work.

In *Ingelarella* the surface pits are elongate, narrow and shallow, and would perhaps be better described as delicate furrows. They are usually broadest and deepest in their median portions, and taper toward each end. In some species, however, some pits are broadest and deepest toward the umbo and taper abruptly posteriorly and gradually anteriorly. Pits commonly transgress the growth laminae. Their size may vary from lamina to lamina, particularly on the anterior part of the shell, probably indicating periods of seasonal growth. There is little doubt, however, that in general the shape, size, and arrangement of the pits are of specific value.

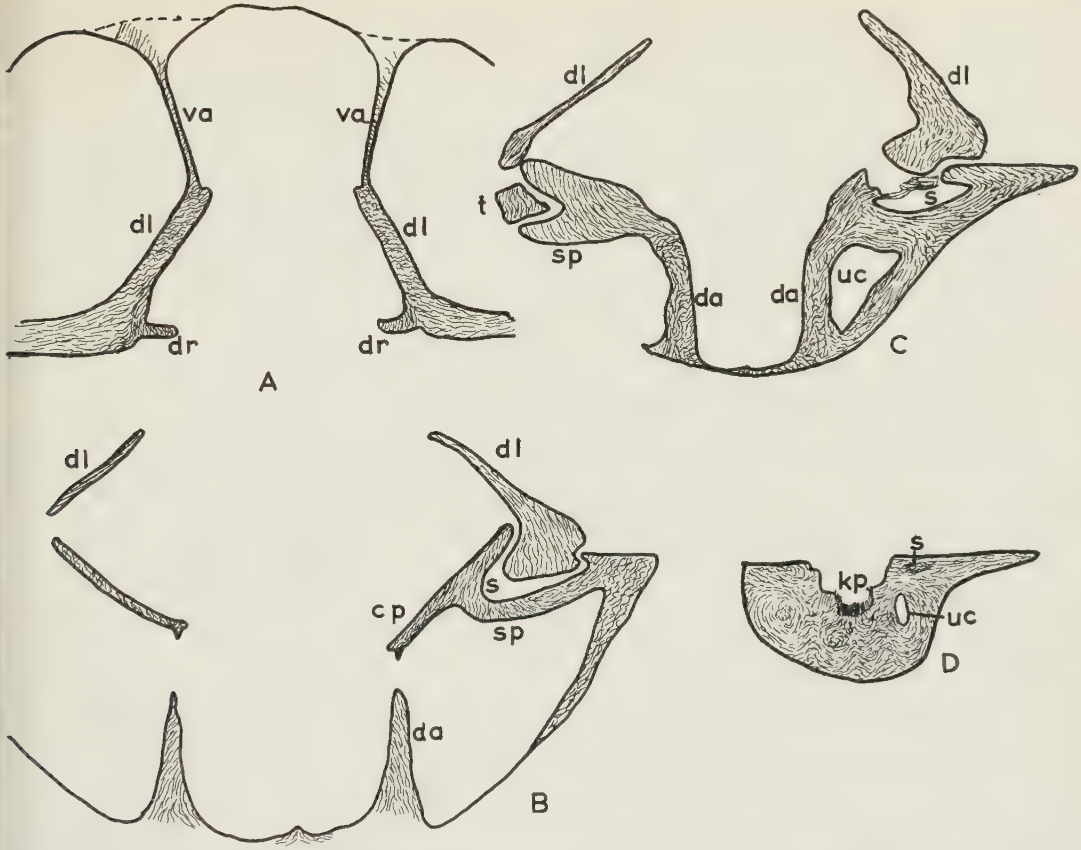
The pits of *Notospirifer* are deeper, coarser, and more closely packed than in any species of *Ingelarella* with which I am acquainted. In addition their outline is also more nearly equidimensional, in some cases being almost circular. The size and shape of the pits varies in some specimens in an irregular manner, e.g. a specimen from Homevale shows sub-circular pits on some portions, oval on others, and diamond shaped on yet others (cf. Etheridge 1919, pl. 28, fig. 2). Other specimens show a weak seasonal variation in size of the pits on the adult stages.



TEXT-FIG. 1. Two diagrammatic sections across the umbonal region of *Ingelarella* illustrating the terminology applied to the internal structures of the Ingelarellinae.

Internal structures. In the apex of the pedicle valve is a central thickening which is continued forward as a very short septum dividing the posterior end of the muscle field. This thickening is continuous with the outer wall of the shell and is composed of irregularly arranged fibres. Contiguous with it apically, but diverging forwards, is a pair of plates, formed as an ingrowth of the outer wall, and composed of curved fibres which sweep forwards and inwards. They are thickest near the umbo and thin out rapidly forwards, where they form a lining to the posterior third of the delthyrial cavity. Their function is not apparent, and they may be merely 'connective' tissue filling in the umbonal area, and hence they are herein referred to as pleromal plates (πληρόω = I fill). The adminicula (Browne 1953, p. 102) lie between the pleromal plates and the outer shell wall and are formed of tissue continuous with the inner-wall layer. The fibres of which they are formed are arranged roughly at right angles to their surface, though there are many irregularities.

At an early stage in ontogeny a thin layer begins to become differentiated on the inner side of the adminicula just inside the delthyrium and along the edge of the cardinal area. From the outset these differentiated portions, which develop into the dental lamellae, carry short processes which line the edge of the delthyrium and extend anteriorly into the teeth. These are referred to as dental ridges. The dental lamellae increase in height and thickness toward the front. Their structure is fibrous, the fibres being arranged



TEXT-FIG. 2. Sections through specimens of *Ingelarella angulata* sp. nov. showing the fibre arrangement in various plates. A, section of the pedicle valve just behind the hinge line; B, slightly oblique section taken through one tooth and anterior to the other; C, slightly oblique section taken posterior to one tooth and through the other; D, section through a brachial valve showing the cardinal process and the very apex of the right dental socket. cp, crural plate; da, dorsal adminiculum; dl, dental lamella; dr, dental ridge; kp, cardinal process; s, socket; sp, socket plate; t, tooth; uc, umbonal cavity; va, ventral adminiculum.

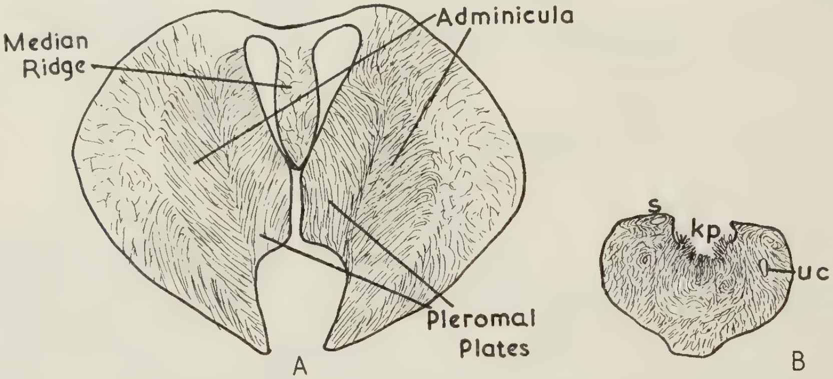
parallel with their length, and their outer surfaces are lined by the adminicula for a greater or lesser distance depending on the species.

The apex of the notothyrial cavity of the brachial valve is lined with a thick fibrous layer, from the inner surface of which the plates of the cardinal process are developed. This layer becomes progressively thinner anteriorly and does not appear to reach the posterior limits of the muscle scars.

The apex of the dental sockets is carried in a distinct fibrous layer lining the cardinal area. This layer is welded on to the outer wall of the shell and the infolded dorsal adminicula. As the sockets develop, a very thin covering plate is retained over their ventral (outer) surface, but the remainder of the socket layer becomes thickened, and a projection from their inner edges forms a carina along the ventral edge of the notothyrial cavity in most species. It is from this carinate portion that the descending lamellae of the spires subsequently develop. Anteriorly, the adminicula, which serve as supports for the socket complexes, decrease in height and the latter become free. The median carina is formed by a slight thickening of the shell.

Genus MARTINIOPSIS Waagen 1883

Type species by subsequent selection of Etheridge (1892, p. 238): *Martiniopsis inflata* Waagen 1883. As Browne (1953) has pointed out, Etheridge made the first formal designation of the type species, though this has been overlooked in favour of the designation of Hall and Clarke (1894).



TEXT-FIG. 3. Sections through specimens of a large undescribed species of *Ingelarella* from the Homevale district showing the fibre arrangement in various plates. A, section through the pedicle umbo showing the median and pleromal plates and the adminicula; B, section of a brachial valve through the lower part of the sockets. Symbols as for text-fig. 2.

Diagnosis. Small Ingelarellinids with length approximately equal to width; hinge line very short and cardinal extremities well rounded; sinus and fold not developed; commissure rectimarginate to sinuate; lateral slopes non-plicate, smooth; surface ornamented with quincuncially arranged pits of unknown shape; ventral adminicula and dental lamellae well developed; dorsal adminicula long and thin.

Remarks. Waagen (1883) placed two species *M. inflata* and *M. subpentagonalis* in his genus *Martiniopsis*, the former being recorded only from the Upper *Productus* Limestone of the Salt Range, while the latter 'seems to be a species characteristic of the lower division of the *Productus* Limestone'. *M. subpentagonalis* was considered to be distinguished by its 'much flatter valves, a more prominent beak and a more distinct cardinal area than *M. inflata* . . .'. Although both dental and crural plates were described by Waagen the details of the internal structure of the genus have remained unknown until recently, when Dr. Ida Browne (1953, p. 103) published serial sections of a specimen from the Lower *Productus* Limestone at Amb. On the basis of a graphical analysis of external characters, an attempt was made to show that *M. subpentagonalis* and *M. inflata* are conspecific, and hence that the figured serial sections, which are from a specimen from the type locality of *M. subpentagonalis*, are in fact typical of the type species. With the information available at present it is, in my opinion, impossible to prove conclusively that these two species are conspecific. However, the work of Waagen (1883) and Browne

(1953) shows that they are similar in external form, ornamentation, and in the presence of ventral and dorsal adminicula, so that there is little doubt that they are congeneric. Though attempts have been made to obtain topotypes of *M. inflata* these have not met with success, and hence I am here interpreting the internal structure of *Martiniopsis* on the sections figured by Browne (1953, p. 101). It is to be noted that no details are yet available on the muscle scars of either valve of the Indian species.

Distribution. In general it has proved difficult to assess the accuracy of many references to *Martiniopsis* because of inadequate illustrations and the lack of descriptive detail concerning internal characters and surface ornament.

Permian species placed in Martiniopsis

Name and reference	*Locality and stratigraphical position*	*Age*
M. inflata Waagen in Waagen (1883)	Upper *Productus* Limestones of Salt Range	Tartarian
M. subpentagonalis Waagen in Waagen (1883)	Lower *Productus* Limestones of Salt Range	Artinskian
M. latouchei Diener in Diener (1911)	'*Fusulina*' Limestone of Kehsi Mansam, Shan States	Tartarian
M. cathaysiensis Grabau in Grabau (1936)	Maping Limestone of Kweichow and Kwangsi	Sakmarian
M. uralica Tscher. *M. orientalis* Tscher. in Tschernyschew (1902)	'*Schwagerina*' Limestone of the Urals	Sakmarian and Artinskian

Doubtfully placed in Martiniopsis

M. uralica Tscher. and *M. orientalis* Tscher. in Mansuy (1913)	*Productus* Limestones of Laos and Tonkin	? Artinskian
M. inflata Waagen in Mansuy (1912)	Yunnan	? Artinskian
M. inflata Waagen. *M. convexa* Tscher. *M. orientalis* Tscher. *M.* cf. *lutugini* Tscher. in Grabau (1934)	Chihsia Limestone of Kweichow	Artinskian
M. subaviformis Grabau in Grabau (1936)	Maping Limestone of Kwangsi	Lower Sakmarian
M. lutugini Tscher. *M. convexa* Tscher. in Tschernyschew (1902)	'*Schwagerina*' Limestone of the Urals	Sakmarian and Artinskian
M. uralica Tscher. *M.* n. sp. ind. aff. *convexa* Tscher. *M. laticollis* Merla in Merla (1934)	Karakorum	Lower Permian
Spirifer (*Martiniopsis*) *talishaoensis* Reed in Reed (1927)	Yunnan	? Artinskian

Not placed in Martiniopsis

M. baschkirica Tscher. *M. b.* mut. *indosiniensis* Mansuy in Mansuy (1913)	*Productus* Limestones of Laos and Tonkin	Artinskian
M. ? *bashkirica* Tscher. *M.* ? *orientalis* Tscher. in Ozaki (1931)	North China	Permian
Martinia nucula Broili, see Branson (1948, p. 418)	Timor	Permian
M. baschkirica Tscher. in Hayasaka (1922)	Manchuria	Permian

M. aschensis Tscher. *M. bashkirica* Tscher. in Tschernyschew (1902)	'*Schwagerina*' Limestone of the Urals	Sakmarian and Artinskian
Spirifer interplicatus Rothpletz var. *bashkirica* Tscher. in Heritsch (1935): see Branson (1948, p. 417)	Lower *Schwagerina* Limestone of the Carnic Alps	Sakmarian
Martiniopsis sp. in McLearn and Kindle (1950, p. 33)	Mt. Merrill, British Columbia	? Permian

The above determinations are made on the basis of the available literature only, except in the case of the last-mentioned form. In this instance the specimens concerned were made available by Dr. Peter Harker of the Canadian Geological Survey. I consider them to belong to the Rostrospiracea.

Occasional specimens from outside the Permian have been referred to the genus. A lower Carboniferous form from Novaya Zemlya was considered to be a *Martiniopsis* by Lee (1909, p. 159), but its multi-plicate lateral slopes, plicate sinus, and the linear arrangement of its micro-ornament, clearly show that its affinities are elsewhere. From the mid-Devonian of Ohio and Nevada and the Upper Devonian of New York come three species which Cooper (1944, p. 329) has tentatively referred to '*Martiniopsis*'. Dr. Cooper has kindly provided me with specimens of '*M.*' *laevis* Hall from the Ithaca Formation of New York. One well-preserved exterior shows a regular and closely set, fine, concentric ornament, crossed by close, very delicate striae. The interior of the brachial valve shows two short plates (no more than 1 mm. in length) immediately beneath the umbo, but it is not clear from the specimens available whether these are adminicula or the result of the direct union of the crural plates with the shell wall. Hall's figures (1867, pl. 39, figs. 3, 5, 6) show a well-developed pseudodeltidium, and fig. 7 shows a marked plication of the anterior portions of the lateral slopes unknown in *Martiniopsis*. In contour and outline this species resembles some species of *Ingelarella*, but there is no doubt that the resemblance is due to homeomorphy.

Martiniopsis thus appears to be restricted in time to the Permian (or possibly to the Uralian and Permian), and in space to the Asian Tethys and its offshoots in the Ural and Cathaysian troughs. In all areas it appears to be associated with warm-water limestone deposits which contain fusulines. It is significant that the genus has not been recorded in the pre-*Productus* Limestone formations of the Salt Range (Sakmarian) which are of a cold-water facies, though it occurs in the Sakmarian limestones of the Urals; and further, no genuine record of it has come from the other cold-water areas of Gondwana.

INGELARELLA gen. nov.

1845 *Spirifer* Sowerby; Morris (in part), p. 281, pl. 15, figs. 5, 5*a*; pl. 16, figs. 1, 4.
1872 *Spirifera* Sowerby; Etheridge (in part), p. 330, pl. 16, figs. 3–5.
1877 *Spirifer* Sowerby; de Koninck (in part), p. 177, pl. 11, fig. 8, pl. 12, fig. 1; p. 179, pl. 10, fig. 11, pl. 11, fig. 10, pl. 16, fig. 1; p. 181, pl. 12, fig. 3; p. 183, pl. 13, fig. 1, pl. 14, fig. 1 (page and plate numbers refer to the English translation of 1898).
?1891 *Martiniopsis* Waagen; Waagen, pp. 131–2, pl. 5, figs. 9*a*, *b*, *c*.
1892 *Martiniopsis* Waagen; Etheridge, pp. 236–41, pl. 11, fig. 14; pl. 9, figs. 13–14; pl. 39, figs. 5–7; pl. 11, figs. 12–13.
1892 *Spirifera* Sowerby; Etheridge (in part), p. 234, pl. 10, figs. 5–7.
1919 *Martiniopsis* Waagen; Etheridge, pp. 184–6, pl. 28, figs. 1, 5–6; pl. 29, figs. 1–2.
?1932 *Spirifer* (*Brachythyris*) M'Coy; Reed, pp. 27–28, pl. 5, figs. 10–12.
1955 *Notospirifer* Harrington; Harrington (in part), pp. 115–17, pl. 23, figs. 3–6, 8–10, 13, 15.

Type species Ingelarella angulata sp. nov., from the Ingelara Shale, Queensland.

Diagnosis. Shells small to large in size; fold and sinus present, but very variably developed, and each with or without a median furrow; lateral slopes smooth or exhibiting varying degrees of plication; pedicle umbo usually high; hinge about two-thirds the maximum width of the valve; shell formed of two layers, the outer usually being of the order of $\frac{1}{25}$ mm. thick, and carrying a series of fine semi-quincuncially disposed short linear depressions; dental lamellae and ventral adminicula present, the latter never lying completely lateral to the folds bordering the sinus; sockets long; crural plates and dorsal adminicula always developed; descending lamellae robust, and spires directed postero-laterally.

Remarks. Martiniopsis Waagen differs from this genus in its lack of a median fold and sinus, its smaller size and the absence of plication on the lateral slopes.

Within the genus three stocks have been recognized, each of which may possibly be worthy of sub-generic rank.

(*a*) The type stock of *I. angulata* which includes species of moderate size with plicate lateral slopes and long to short dorsal adminicula.

(*b*) A group of larger species with non-plicate or very weakly plicate lateral slopes and long dorsal adminicula. This is typified by the form illustrated as *Martiniopsis sp.* ‘a’ from Ingelara (Campbell 1953).

(*c*) A group of species of the *I. oviformis* (M‘Coy) type, with strongly inflated and elongate shells, deeply plicate lateral slopes, and weak to strong dorsal adminicula.

The division between stocks (*a*) and (*b*) may not be definite, but study of larger collections will be necessary before the issue can be clarified. It may be that some of the species included in stock (*a*) have evolved independently from stock (*b*).

Distribution. The genus occurs throughout eastern Australia in rocks which are thought to range in age from Sakmarian to Kazanian. It frequently occurs in profusion, and is one of the most widespread genera in our Permian deposits.

Waagen (1891) described a single specimen referred to *Martiniopsis darwini* (Morris) from the Speckled Sandstone of the Salt Range, India. The specimen is a small brachial valve. None of the internal characters are described, and hence it is impossible to assign the form definitely to *Ingelarella*, but Waagen’s statement that ‘under the lens one can observe at places a trace of the granulation of the shell, characteristic of the genus, but so far deteriorated by weathering that the grooves in which the granules had been placed have become elongate instead of being round’, suggests that it may well belong to that genus.

The fragmentary specimen from the Zewan Beds of Kashmir referred by Diener (1899) to *Martiniopsis* sp. ind. aff. *subradiata* (Sowerby) is badly distorted, and from the description it appears that Diener was not certain even whether it was a pedicle or a brachial valve. It is said to have a very faint radial ornamentation and a punctate and fibrous shell structure. The interpretation of this specimen from the data available is a virtual impossibility.

Reed (1932) has referred two incomplete brachial valves from the Agglomeratic Slate of Kashmir to *Spirifer* (*Brachythyris*) *darwini* Morris. The figures and description certainly suggest the brachial valve of an *Ingelarella*, except that Reed claims that the shell is minutely punctate, but without the details of the pedicle valve one cannot be certain of this determination.

The Argentinian specimens referred by Harrington (1955) to *Notospirifer darwini* (Morris) closely resemble *I. angulata* sp. nov. The Bonete Formation, from which these fossils come, is considered to be Sakmarian or Artinskian in age. Further discussion of these specimens is included under *Notospirifer*.

Fletcher (1952) has assigned some poorly preserved specimens from the Productus Creek area of New Zealand to *Spirifer* cf. *glaber* Dana (*non* Martin) from N.S.W., this species being an *Ingelarella*. Trechmann (1917) had previously placed specimens from the Maitai Series in the Tasmanian species *Ingelarella subradiata* (G. B. Sowerby).

Three Russian species have been compared with Australian Ingelarellinids—*Spirifer sokolovi* Tscher., *S. supracarbonicus* Tscher., and *Brachythyris kumpani* Yan. (see Tschernyschew 1902, pp. 552-4; Yanischevsky 1935, p. 68). All of these forms are very similar externally to various species of *Ingelarella*. However, in the case of both *S. sokolovi* and *S. supracarbonicus* the external ornament appears to consist of growth lines only, and the internal structure remains virtually unknown. Had the Ingelarellinid ornament been present Tschernyschew would no doubt have observed it, since he did so on *Martiniopsis*. The presence of weak folds in the sinus relates these species to *S. ufensis* and *S. uralicus* (both of which have dental lamellae and ventral adminicula), as was suggested by Tschernyschew himself, and excludes them from *Ingelarella*. Probably *B. kumpani* also belongs to the same species group.

Distribution. In Queensland *Ingelarella* ranges from the lowest to the highest known marine Permian beds, i.e. from the Dilly Formation of the Springsure area to the '*Martiniopsis*' bed above the *Streptorhynchus* zone at the northern end of the Bowen Syncline. It has a comparable range in New South Wales. Current correlations suggest that the time interval involved is from about the Sakmarian to the Kazanian.

In both Pakistan and Argentina the genus appears to be restricted to the lower part of the Permian, but in Argentina this range will probably have to be extended upwards when the faunas of the Permian are better known.

Genus NOTOSPIRIFER Harrington

Type species by original designation: *Spirifer darwini* Morris, from Glendon, Hunter Valley, N.S.W.

Diagnosis. Shell small to medium size; much broader than long; hinge line three-quarters to five-sixths of the maximum width; cardinal extremities rounded; sinus and fold present; fold rounded, flattened, or bearing a shallow median groove; lateral slopes deeply plicate, with three to six plicae; surface with deep, closely packed, sub-circular or slightly elongate pits; thick dental lamellae supported on short, widely divergent adminicula; thick crural plates, but supporting adminicula very weak or absent.

Remarks. Harrington (1955) in describing his new genus figured the syntype BB. 6243 B.M. of *Spirifer darwini* Morris, but he did not formally nominate a lectotype for the species. Therefore I here designate BB. 6243 B.M., from Glendon, N.S.W., figured

Harrington (1955, pl. 23, figs. 7, 11, 12, 14), and figured herein (Pl. 56, figs. 1*a–c*), as the lectotype of *S. darwini* Morris.

Two trips have been made in an attempt to rediscover the locality at Glendon from which Strzelecki collected the types of *S. darwini*, but without success. The type specimens are in a ferruginous sandy matrix. On the bank of the Hunter River in front of Glendon Homestead is an outcrop of the Muree Formation from which I have collected several specimens of *Ingelarella* in a very ferruginous sandy matrix, but no specimens comparable with either of the syntypes has been found. Thus I have had to interpret the species on the basis of the Strzelecki specimens, which I have seen at the British Museum. Harrington has already described these using plaster casts of the originals and notes provided by Dr. Muir-Wood.

As recorded by Harrington (p. 116), Muir-Wood believes the specimens show 'obscure traces of spines which must have covered the whole surface'. In my opinion the surface ornament is not shown on either specimen, and the structures described as spine traces are the result of irregular decortication of the shells. In this connexion two further points are of significance. The typically Ingelarellinid ornament figured by Harrington (1955, pl. 23, fig. 15) is described in the text as 'lamellose-fimbriate' (p. 117), and although Muir-Wood believes that obscure traces of spines are present, no details of the spines themselves have been observed (Harrington, p. 116).

In my opinion the two syntypes are not congeneric. Specimen BB. 6244 has the pedicle umbo broken off, but it is apparent from the general contour of the posterior portion of the valve that the umbo was quite high. The plicae of the lateral slopes are low. The interior of the pedicle valve is not well exposed, but it is almost certain that the muscle field is narrow and bounded by long adminicula lying within the folds bordering the sinus. The brachial valve has relatively long widely divergent dorsal adminicula. The specimen almost certainly belongs to *Ingelarella*. Dr. Cooper, U.S. National Museum, has kindly sent plaster casts of specimens assigned to *S. darwini* in the collection from Glendon described by Dana (1849). This specimen (Pl. 56, figs. 3*a*, *b*) compares favourably with BB. 6244 in all features including the dorsal adminicula, which diverge outside the first plica lateral to the fold in a way unobserved in any other species. I am convinced that the two specimens are conspecific. The ventral adminicula are well exposed and confirm the tentative observation made on these structures in BB. 6244. Unfortunately no surface ornament is preserved.

The lectotype BB. 6243, on the other hand, has a very low pedicle umbo, and a very transverse outline. The folds on the lateral slopes are rather strong. The ventral adminicula are short and widely divergent, lying outside the folds bordering the median sinus. The dorsal adminicula, if present, must be very short. All of the species (four in number) with this combination of characters which have come under my notice also have a surface ornament of rather deep pits. In the absence of direct evidence in support of this from the actual lectotype, and in view of my failure to discover topotypes, the surface characters of these species have been attributed to *N. darwini* (Morris).

Distribution. No species yet described from outside eastern Australia is considered to belong to this genus. As is indicated in the discussion on *Ingelarella*, the Indian forms referred to *Martiniopsis darwini* (Morris) by Waagen (1891) and *Spirifer* (*Brachythyris*) *darwini* Morris by Reed (1932), and the Argentinian specimens referred to the same species by Harrington (1955), are considered to belong to *Ingelarella* rather than to *Notospirifer*. In Queensland the genus ranges from the Homevale Beds to the *Streptorhynchus* zone, i.e. Sakmarian–? Kazanian. Its range in the other eastern States is unknown.

SIMILAR GENERA

The spiriferid stock has at several times developed smooth or pauci-plicate homeomorphic groups (see Buckman 1908), many of which have, at some time or another, been referred to *Martiniopsis*.

Warrenella Crickmay, from the Middle and Upper Devonian of North America, has the conformation, smooth fold and sinus and lateral slopes, thickened umbo and dental lamellae of an *Ingelarella*, and there are also resemblances in the fine surface ornament which in *Warrenella* consists of 'short (0·1 mm.) radial threads disposed in concentric groups 1·5 mm. apart' (Crickmay 1953, p. 598). Yet the peculiar mode of thickening in the pedicle umbo, the presence of a deltidium, the unusually thickened brachial valve, and the ridged rather than pitted micro-ornament arranged on a linear rather than a quincuncial pattern, show beyond reasonable doubt that this genus is genetically quite unrelated to the Ingelarellinids.

The relationship of *Martinia* to *Martiniopsis* has been discussed by several authors since Waagen (1883), and notably by Etheridge (1892, p. 237). There is no doubt that the two genera can be distinguished by the presence or absence of ventral adminicula, and by the absence of a pitted surface layer in *Martinia*, but there may also be differences in the intimate structure of the shell substance. For example, the species from the Permian of Mongolia assigned to *Martinia* by Grabau (1931) all have a smooth surface except for fine irregular concentric growth lamellae, but the exfoliated surface has numerous radiating striae which give rise to delicate pustules where they cross the growth lines. This has never been observed in any Australian Ingelarellinids.

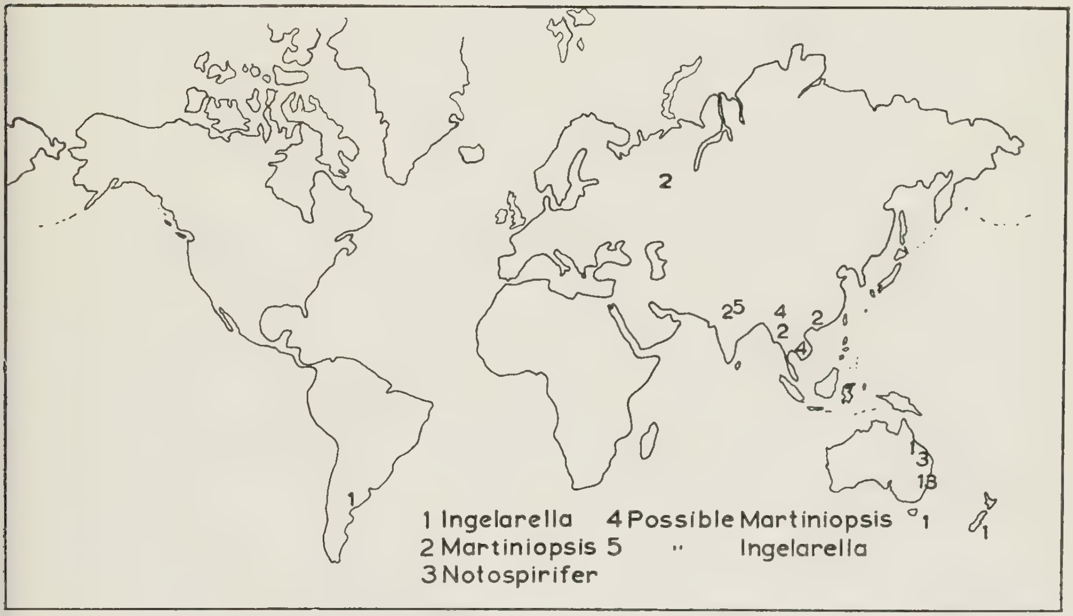
From the lower Carboniferous of China comes a large group of species referred to the genus *Martiniella* Grabau, which in external form and the presence of ventral adminicula resembles *Martiniopsis*. On the evidence available at present they may be distinguished from this latter genus by the absence of dorsal adminicula, and by the presence of a finely striate micro-ornament (Chu 1933, p. 51).

Of greater interest is the genus *Eomartiniopsis* Sokolskaya, from the Tournaisian of the Moscow Basin. Both in general form and the development of plates in each valve, this genus resembles the *Martiniopsis*. It is difficult to assess the relationships of the surface ornament which is said to be finely pitted. The semi-quincuncial arrangement, however, does not resemble that of either *Ingelarella* or *Notospirifer*. The possibility must still be entertained, however, that this genus belongs to the Ingelarellinae.

To accommodate species of the type previously referred to *Martiniopsis baschkirica* Tschernyschew and *M. aschensis* Tschernyschew, Fredericks (1919) erected the genus *Elivella*. Both of these species are characterized by a very narrow fold and sinus, multiplicate lateral slopes and a very finely striate surface ornament. In the case of *M. baschkirica*, Tschernyschew records that the folds bordering the sinus bifurcate at about the mid-length of the valve and that the test exhibits a fine 'punctstructur'. These features are sufficient to exclude *Elivella* from the Ingelarellinae.

Mentzelia Quenstedt has as type species *Spirifer medianus* Quenstedt from the Muschelkalk of Silesia, but Douglas has described a Permian species, *M. persica*, from

Iran (Douglas 1940). In external form and the presence of dental lamellae this species is not unlike *Martiniopsis*, but internally it is distinguished by the presence of a high median septum in the pedicle valve, and a thick hinge plate of a kind unknown in the Ingelarellinae, in the brachial valve. In addition, the surface is described as 'smooth with occasional concentric growth-lines' (Douglas 1940, p. 332), and the shell structure is said to be fibrous and impunctate. Certain Triassic species ascribed to *Mentzelia* are, however, claimed to be punctate (Trechmann 1917, p. 228).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1
1 Ingelarella 4 Possible Martiniopsis
2 Martiniopsis 5 " Ingelarella
3 Notospirifer

TEXT-FIG. 4. Distribution of the genera of the Ingelarellinae.

Ingelarella angulata sp. nov.

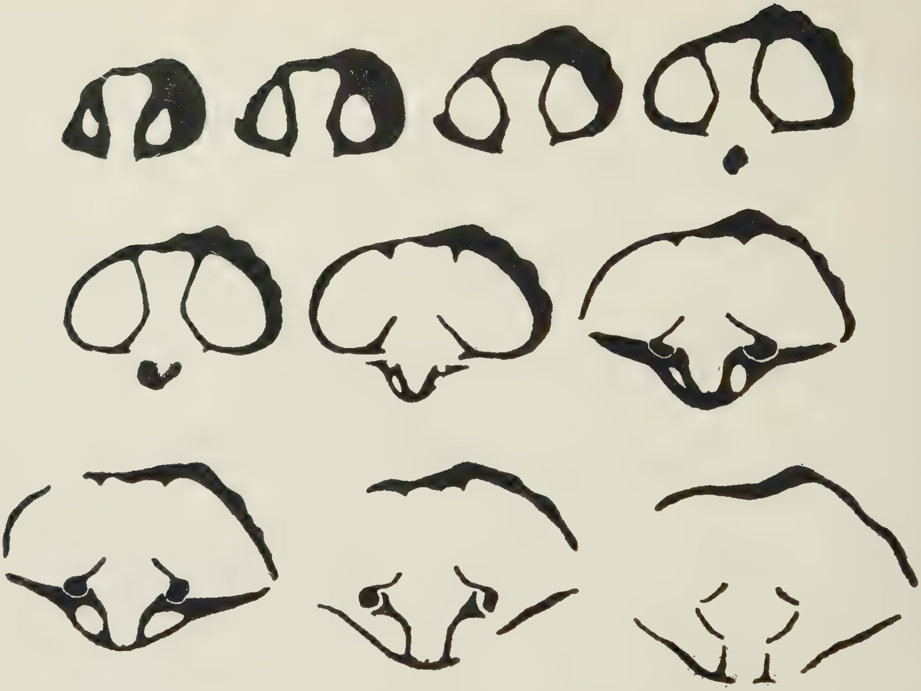
Plate 56, figs. 4*a–c*; Plate 57, figs. 1–5

1953 '*Martiniopsis*' sp. b, Campbell, p. 10, pl. 4, figs. 4–9; pl. 5, figs. 4–6.

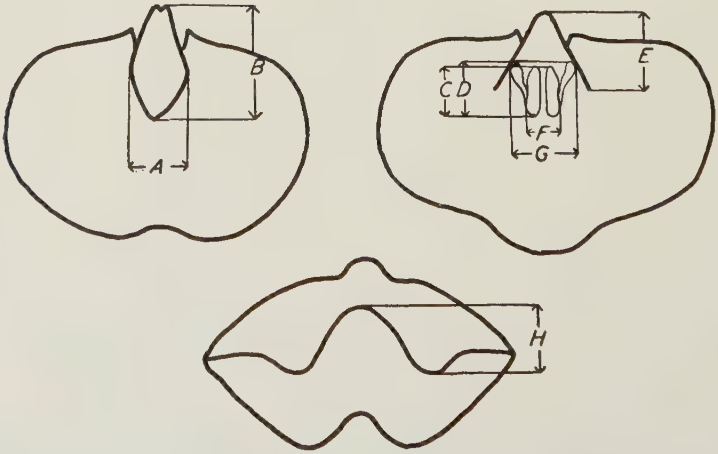
Holotype. F. 14295, U.Q.; from Ingelara Shale, Dry Creek, $\frac{1}{2}$ mile upstream from the road crossing, Ingelara Station, south-west of Springsure, Queensland: *paratypes*, F. 14294 and F. 14296–7; F. 15695–F. 15697 and F. 24834 and F. 24837, U.Q.

Diagnosis. Medium-sized, plicate shells usually with an open V-shaped median sinus; fold bearing a median furrow; ventral adminicula long, thin and curved inwards anteriorly; dorsal adminicula slender, upright, and extending one-quarter to one-third the length of the valve.

Description. The shells are of medium size for the genus, with a moderately convex pedicle valve and a somewhat less convex brachial valve. The hinge line is approximately five-eighths of the maximum width of the shell.



TEXT-FIG. 5. Serial sections of a topotype of *I. angulata* sp. nov. taken at 1 mm. intervals. ×1.



TEXT-FIG. 6. Diagrams illustrating the method of taking the measurements listed in the table of dimensions. A = width ventral muscle field; B = length ventral muscle field; C = length central dorsal adductors; D = total length dorsal adductors; E = length dorsal adminicula; F = width central dorsal adductors; G = total width dorsal adductors; H = height fold. Diagrams are of an internal mould.

The ventral valve is most convex towards the incurved umbo. The dental ridges are thin but wide. The median sinus is clearly defined, the transverse sections being open V-shaped in most specimens, though in others there is a tendency towards a flatter bottom. A shallow median groove is invariably present. The sinal angle averages 24° (range 18–30° over seven specimens). The gently convex lateral slopes each carry four low, rounded plicae which rapidly diminish in size laterally, the most lateral one frequently being indistinct.

The brachial valve is almost oval in outline and its length is approximately three-quarters of the width. It is usually evenly convex longitudinally, but it may be slightly more convex toward the umbo. The lateral slopes are gently convex. The median fold is of moderate height, not breaking the general contour of the valve, and its central portion is occupied by a shallow furrow.

Because of the nature of the preservation the surface pits are rarely seen.

Interior. The pedicle valve has only slightly thickened umbonal shoulders. The ventral adminicula extend approximately one-third the length of the valve and tend to curve together toward their anterior tips. Transverse sections show the planes of the adminicula converging toward each other at angles between 10° and 35°. In these sections the convergence of the dental lamellae varies according to the position of the section, the angle at a position just posterior to the teeth being in the vicinity of 80°–90°. The dental lamellae are relatively unthickened and on their outer surfaces the extension of adminicular tissue is never thick. The teeth are large bulbous structures which are hooked inwards. Preservation in a hard calcareous sandstone which does not permit the exposure of internal detail by cleaning or etching, makes the muscle field difficult to observe, but it is known to be long and narrow.

Dimensions (in mm.)

Length	*Width*	*Height*	*Length brachial valve*	*Height fold*	*Length ventral muscle field*	*Width ventral muscle field*	*Length central dorsal adductors*	*Width central dorsal adductors*	*Total length dorsal adductors*	*Total width dorsal adductors*	*Sinal angle*	*Length dorsal adminicula*
Mt. Coma, near Mt. Britton												
51	65	33	43	8	. .	11	. .	. .	. .	. .	. .	17
50	53	32	42	12	*c.* 26	13·5	. .	3·5	. .	9·5	. .	19
48	54	. .	38	9	*c.* 23	8·5	. .	. .	. .	. .	. .	18
46	57	28	40	6·5	20	9	12	2·5	17	8	23°	17
40	*c.* 52	26	35	7	18	8	9	2·5	12	6	. .	18
. .	47	25	. .	. .	. .	9	9	2	10	5·5	. .	12
33	40	19	29	4	14	8	. .	2	. .	5	24°	12
Dry Creek, Ingelara												
. .	*c.* 65	. .	. .	. .	*c.* 25	*c.* 8	. .	. .	. .	. .	. .	24
49	60	34	45	10	*c.* 20	7	. .	. .	. .	. .	18°	13
40	51	32	35	9	. .	. .	. .	. .	. .	. .	23°	. .
35	40	21	31	5	. .	. .	. .	. .	. .	. .	23°	11
30	34	21	28	7	. .	. .	. .	. .	. .	. .	26°	. .

The dorsal adminicula are long and tapering, extending from one-quarter to one-third the length of the valve. They diverge at angles of from 10° to 15° along the floor of the valve. In transverse section they are slightly divergent in the umbo, but they rapidly become almost vertical except for their ventral edges which are slightly flexed outwards. Anterior to their point of origin the descending lamellae are set at about 45° to each other, but as they descend they gradually tend to become parallel. The spires are formed of approximately twenty volutions each. The central adductor scars are apparently rather narrow, but the details are not visible. They are separated by a fine, sharp keel. The cardinal process consists of numerous fine platelets within the notothyrial cavity. There is no sign of a boss or projection for the support of this structure. Towards the front of both valves there are numerous, closely set radial markings which are apparently pallial in origin. They are better preserved on the Mt. Coma specimen described below (see Pl. 57, figs. 3, 5).

Remarks. The population from the type locality is very variable particularly with respect to height of the shell, the degree of development of the plicae, and the shape of the sinus.

There is a resemblance to one of the syntypes (BB. 6244) of *Spirifer darwini* Morris, but this latter form is distinguished by its shorter, more divergent dorsal adminicula, its narrower median fold, and shallower, flatter bottomed sinus.

Specimens from other localities. Specimens probably referable to this species have been obtained from Mt. Cona (Mt. Coma) northwest of Homevale Station, via Nebo, on the

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EXPLANATION OF PLATE 56

Figs. 1–4 are natural size; Figs. 5–12 are ×5.

Figs. 1*a–c*. *Notospirifer darwini* (Morris). Ventral, dorsal, and anterior views of a plaster cast of the lectotype. Note the very short and widely divergent ventral adminicula; BB. 6243 B.M., from Glendon, Hunter Valley, N.S.W.

Figs. 2–3. *Ingelarella sp.* 2*a–c*, Ventral, dorsal, and anterior views of the second of Morris's syntypes of *Spirifer darwini*, BB. 6244 B.M., from Glendon, Hunter Valley, N.S.W. 3*a–b*, Ventral and posterior views of a plaster cast of a specimen collected by the Wilkes Expedition from Glendon, and referred by Dana to *Spirifer darwini*, 3634 U.S. National Museum.

Figs. 4*a–c*. *Ingelarella angulata* sp. nov. Ventral, dorsal, and anterior views of a small paratype from the type locality, F. 14297 U.Q.

Figs. 5–7. *Notospirifer spp.* Three undescribed species. 5, Small patch of surface shell showing the almost equidimensional surface pits filled with white matrix; F. 21945 U.Q. 6, External mould of part of the shell surface showing the infillings of the deep, densely packed pits. These infillings appear to be more or less lozenge shaped over most of the surface due to the fact that they are directed at an angle to the shell and hence have not been photographed end-on. In the bottom left-hand corner they are almost end-on; F. 3055 U.N.E. 7, External mould of part of shell surface. Similar remarks to those above apply; F. 15826 U.Q.

Figs. 8–12. *Ingelarella spp.* Five undescribed species. 8–9 and 11–12 are external moulds, while 10 is the actual shell surface. Note the variation in size, shape, and density of the pits. 8, F. 3228 U.N.E. 9, F. 3111A U.N.E. 10, F. 15686 U.Q. 11, F. 2992B U.N.E. 12, F. 3318 U.N.E.

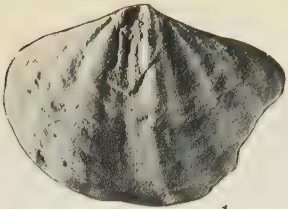
Fig. 13. *Notospirifer sp.* Thin section across the anterior part of the shell of the species shown in fig. 7 above. What appears to be a fringe of bristle-like spines is the result of oblique sectioning of the surface pits. ×3·2.

Fig. 14. *Ingelarella sp.* Thin section of the lamellar layer of a shell showing some of the spicular structures mentioned on p. 335. ×40.

EXPLANATION OF PLATE 57

All specimens natural size.

Figs. 1–5. *Ingelarella angulata* sp. nov. 1*a–c*, Ventral, dorsal, and anterior views of the holotype, F. 14295 U.Q. 2*a–b*, Dorsal and ventral views of an internal mould of a paratype from the type locality, F. 24834 U.Q. 3, Dorsal view of an internal mould of a paratype from the type locality, F. 24837 U.Q. 4*a–c*, Ventral, dorsal, and anterior views of a paratype from the type locality with the shell partly removed, F. 15696 U.Q. 5*a–c*, Dorsal, ventral, and anterior views of an internal mould of a paratype from Mt. Coma, F. 2126 G.S.Q.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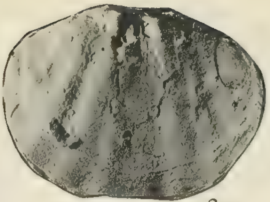
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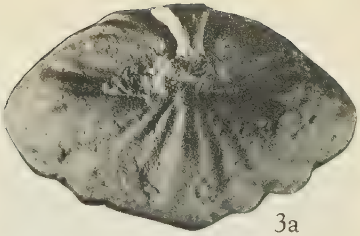
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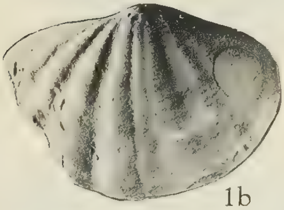
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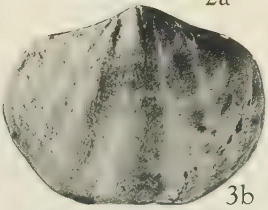
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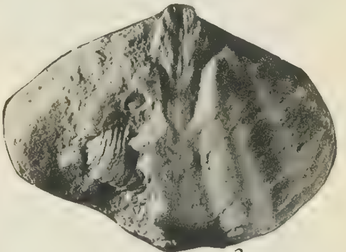
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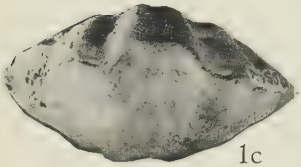
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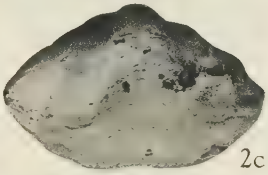
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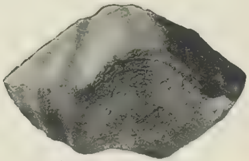
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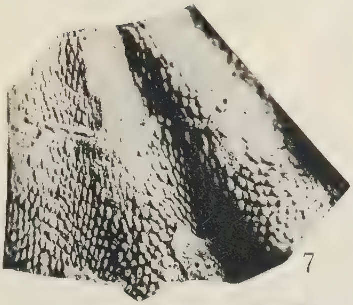
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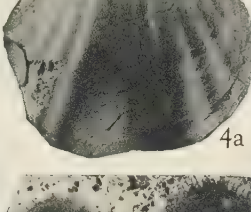
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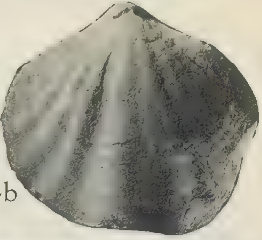
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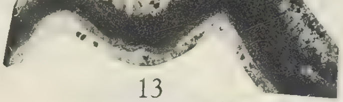
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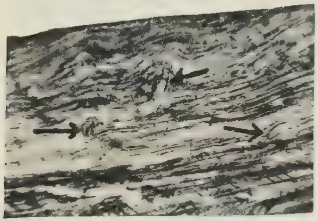
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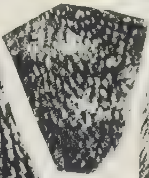
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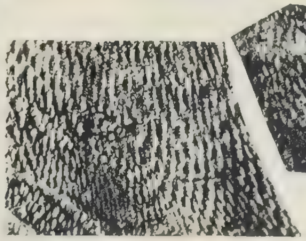
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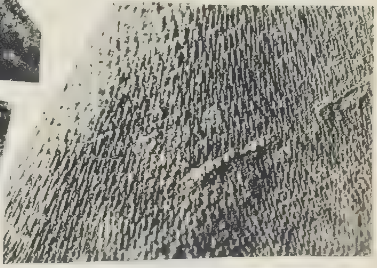
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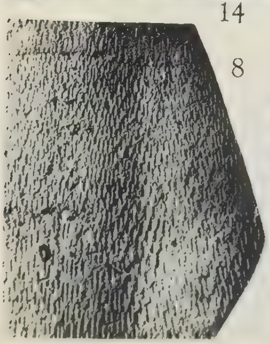
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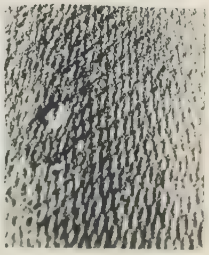
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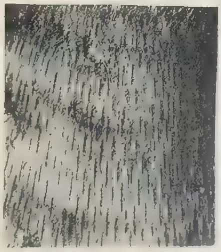
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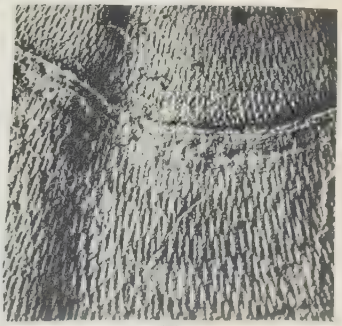
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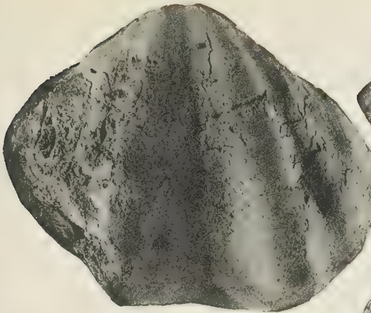
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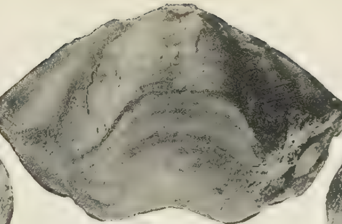
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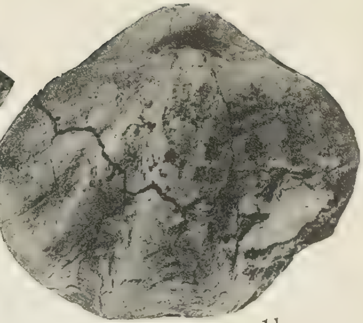
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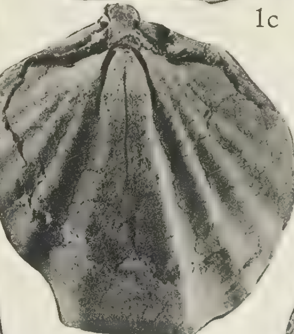
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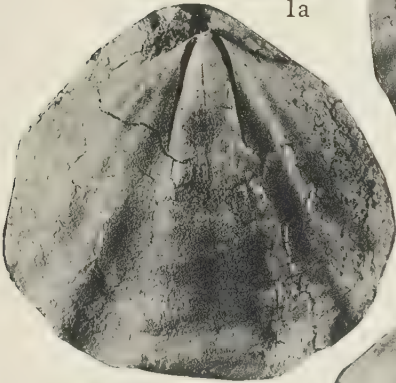
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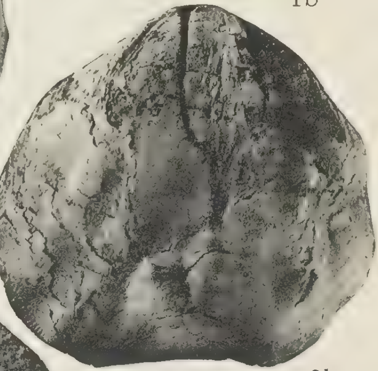
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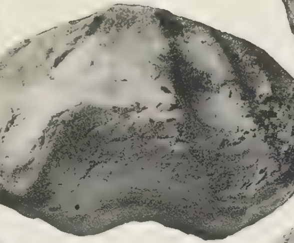
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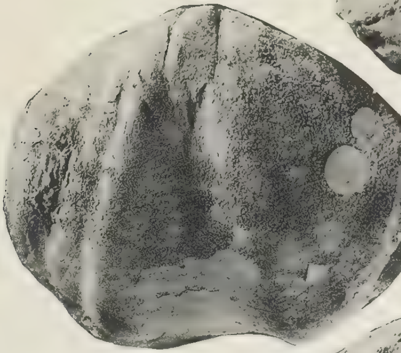
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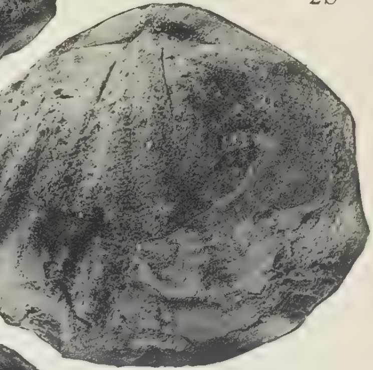
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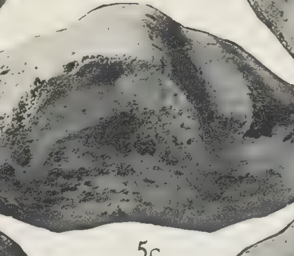
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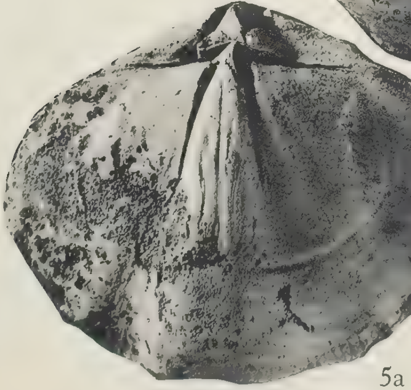
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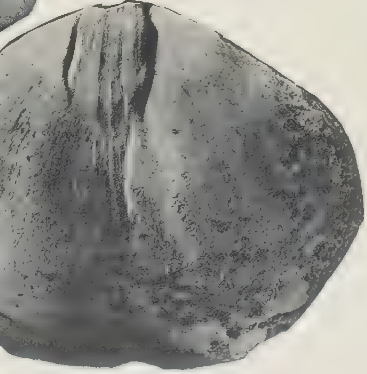
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CAMPBELL, *Ingelarella angulata*

eastern limb of the Bowen Basin. This population differs from the types in its much higher proportion of specimens with shallow flat-bottomed sinuses, as well as the weaker plication of the lateral slopes, and the weaker development of the median groove on the fold. However, even in these characters there is a considerable overlap between the two populations, and there is no doubt that they are closely related. Several features not shown on the types are exhibited by these specimens. The delthyrial angle ranges from 60° to 70° (seven specimens) with a mean of 63°. The adductor scars of the pedicle valve are always 2–3 mm. in width, but the diductors are variable. The adductor scars of the brachial valve are distinctly paired. The central pair is long and narrow and is situated with its posterior edge between one-quarter and one-fifth of the total length of the valve from the edge of the cardinal process. The postero-lateral scars are also very narrow, separate from the central pair within 2 mm. of their anterior edge, and are either parallel or slightly diverging. Their posterior extremities are acute and in adults extend from 2 to 4 mm. behind the central scars. The form of this muscle field is quite distinctive. One specimen has almost 100 plates in the cardinal process. The median ridge is weak.

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THE TYPE SPECIES OF THREE UPPER PALAEOZOIC PUNCTATE SPIRIFEROIDS

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ABSTRACT. The type species of *Spiriferellina* Fredericks, *Reticulariina* Fredericks and *Punctospirifer* North are redescribed from type material.

INTRODUCTION

TO date eight genera of Upper Palaeozoic punctate spirifers have been erected. Two of them, *Crenispirifer* Stehli 1954 and *Altiplectus* Stehli 1954, are well known from modern work. Interpretations of the other genera are many, but all lack authority because of inadequate knowledge of the type species.

In the case of *Paraspiriferina* Reed, erected as a subgenus of *Spiriferina* to embrace *S. multiplicata punjabensis* Reed and *S.* (*Paraspiriferina*) *ghundiensis* Reed, and *Callispirina* Cooper and Muir-Wood (type species *Spiriferina ornata* Waagen), the original diagnosis and descriptions are concerned only with the general form of the shell, and the arrangement and number of the plicae. Information on the surface ornament and interior is either completely lacking or is very vague. The type species come from the Salt Range. The genera remain virtually uninterpretable.

The genus *Spiriferinaella* Fredericks (type species *Spiriferina artiensis* Stuckenberg) is very poorly known, but it is unlikely to be confused with any of the other genera because of its very transverse outline, few low plicae, denticulate hinge, and deep denticle grooves on the pedicle cardinal area.

Reticulariina Fredericks 1916 (type species *Spiriferina spinosa* Norwood and Pratten, from the Mississippian Chester Series of Illinois) has been relatively well known from the work of Hall and Clarke (1893) and Weller (1914). It is easily distinguished from the other described genera by the large hollow spines scattered over the surface. Difficulties have recently arisen, however, in that several species of Permian age from South America and India (Chronic 1953; Reed 1944) have been assigned to the genus primarily on the basis of the presence of coarse spines, without adequate comparison of other features.

The two genera most often confused in the literature are *Spiriferellina* Fredericks 1919 (type species *Terebratulites cristatus* Schlotheim from the Zechstein of Germany) and *Punctospirifer* North 1920 (type species *Punctospirifer scabricosta* North from the Viséan of England). Neither of the authors concerned appears to have been aware of the work of the other, and their papers were published at almost the same time. The early revisers of the group concluded that there was an overlap between the two genera as they were originally defined, such, for example, as was pithily expressed by Paeckelmann's '*Punctospirifer*+paläozoische Formen von *Spiriferina* s. str. North sind = *Spiriferellina* Fred . . .'. Muir-Wood (1948, pp. 63–64) concluded that *Punctospirifer* may be distinguished from *Spiriferellina* 'in having more numerous and less angular plications on the lateral slopes, and in having a more flattened, broader median fold, and shallower

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sinus. In *Spiriferellina* the cardinal area is not sharply demarcated from the lateral slopes. The concentric lamellose ornament is more prominent in *Punctospirifer*. There are also considerable differences in the internal structure of the two genera.' As will be seen from this, the differences consist entirely in the relative degree of development of certain characters, except perhaps in the case of the internal differences, the nature of which have never been made explicit.

The present work has been concerned with the redescription of the type species of *Spiriferellina*, *Reticulariina*, and *Punctospirifer*. In the case of *Spiriferellina cristata* I have been able to examine the syntypes, as well as several specimens from the same horizon as the syntypes at Pössneck. The holotype, paratypes, and numerous topotypes of *Punctospirifer scabricosta*, and several topotypes of *Reticulariina spinosa* as well as other specimens from the Chester Series at Paint Creek, have been examined.

I have not been concerned with the definition of genera as such, but only with the type species, and in this way I have hoped to provide a basis for wider discussion.

Punctospirifer scabricosta North

Plate 58, figs. 1–10; Plate 60, figs. 1, 2

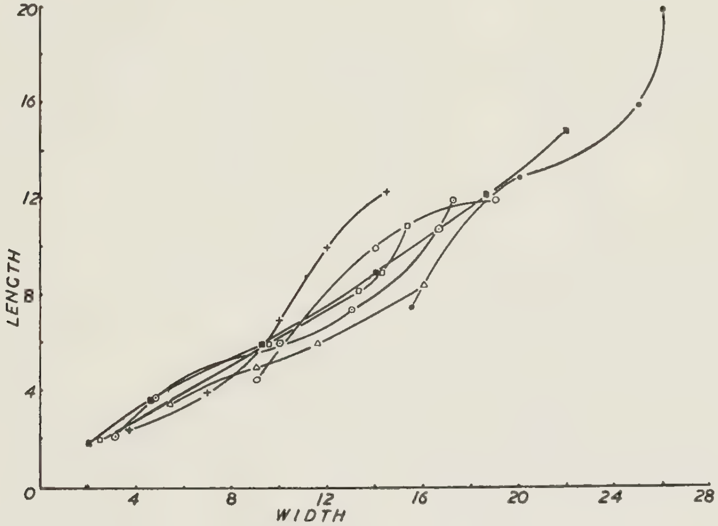
Material. Holotype 64285 G.S.M. from Viséan, Ashfell Edge, Westmorland, England. About twenty topotypes G.S.M., and about fifty topotypes S.M.

Description. The shell at the adult stage is transverse, with sub-rectangular to moderately acute or even faintly mucronate cardinal extremities. At the earliest stages (up to *c.* 5 mm. in width) the extremities are slightly rounded, following which they gradually become angular and then slightly mucronate. This stage may persist through to the adult, or as is more common, the mucros are gradually reduced and sub-rectangular extremities are produced. The pedicle cardinal area is high, the distance between the tips of the two umbones reaching as much as half of the total shell length. In most cases this area is concave immediately beneath the umbo, but flattens out towards the hinge, where it lies almost at right angles to the plane of the commissure. In some specimens, however, the relative rates of deposition on the hinge and commissure remains constant throughout growth so that the area is more or less planar. This combination of high cardinal area and extended hinge line throughout all but the earliest growth stages produces the prominent, sharp, cardinal ridges so often regarded as diagnostic of *Punctospirifer*. The cardinal ridges, of course, are merely the loci of the cardinal extremities during growth. The surface of the cardinal area carries growth lines, often crossed at right angles by very weak lineations. There is no indication, however, of denticle grooves.

The delthyrium is quite uncovered and is bordered by the prominent dental flanges which are at a slightly lower level than that of the cardinal area. The delthyrial angle averages 29° (range 25° to 32° for six specimens). The sinus is deep and V-shaped in transverse section, and often there is a weak median furrow in it. The sinal angle averages 27° (range 23° to 32° for six specimens). There are usually eight or nine well-rounded and regularly spaced plicae on each of the lateral slopes in adults.

The brachial valve is only moderately convex in anterior profile and is almost flat along the crest of the fold in lateral profile. The fold is prominent with steep sides and rounded crest, while the form of the plication in the commissure is high and either well rounded or more commonly sub-ogival.

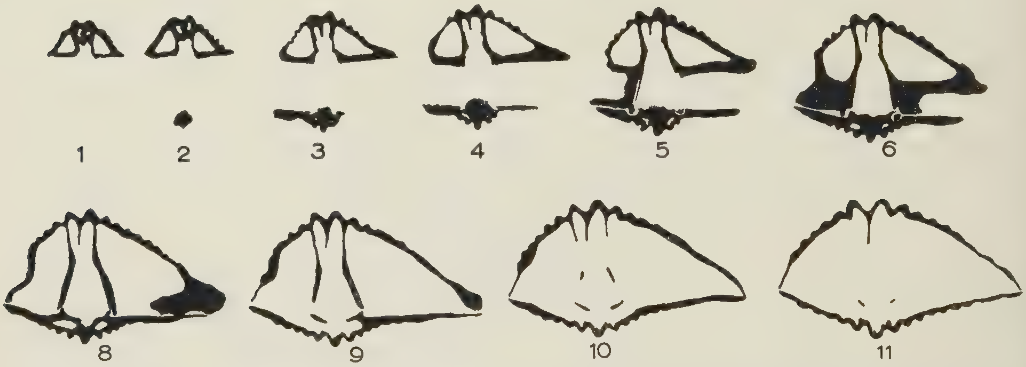
The whole outer surface of the shell, apart from the cardinal areas, is covered with fine, closely spaced imbricating lamellae. There are, of course, irregularities of growth shown on the surface as accentuated aggregates of growth lamellae, but taken by and large the general impression is one of regularity and close spacing. Crossing the lamellae is a series of very fine radial threads which are often in line on adjacent lamellae, so that they could well be called radial lirae. They number 15 to 22 per mm., and are similarly spaced over the whole surface. On the posterior portions of some specimens they seem to be slightly raised into extremely minute projections, causing an almost imperceptible serration of the lamellar edge. This, however, is very rare. No sign of spines or spine bases has been observed. In the bottom of the sinus and inter-plical depressions the lirae are truly radial but they fan out up the sides. The crests of the plicae are invariably worn and the lirae are obliterated.



TEXT-FIG. 1. Plot of length/width (in mm.) of pedicle valves of *P. scabricosta* to show the variation during individual ontogenies.

Interior. The dental lamellae are low, reaching a maximum depth of about one-third the distance from the umbo to the tooth, and gradually taper from that point to the hinge. Along their inner face there is usually a rather sharp flange. They are quite thick in comparison with the adminicula which extend *c.* one-third of the length of the valve along the floor from the umbo. They invariably run down the furrow between the first and second plicae from the sinus. The median septum runs approximately half the length of the valve. It originates in the umbo in a very small, slightly elongate callus of variable size, and increases gradually in size to its sharp antero-dorsal tip where it is slightly undercut and drops away in a sharp curve to the shell wall. In some specimens its junction with the floor of the valve is quite angular while in others it is a smooth curve. The arrangement of the muscle scars has not been determined. In section, however, it is seen that secondary deposition took place well up the sides of the median septum and there is often an abrupt break at the dorsal edge of this deposition. It is probable that this secondary material was laid down on the site of adductor attachment (see text-figs. 2, 3).

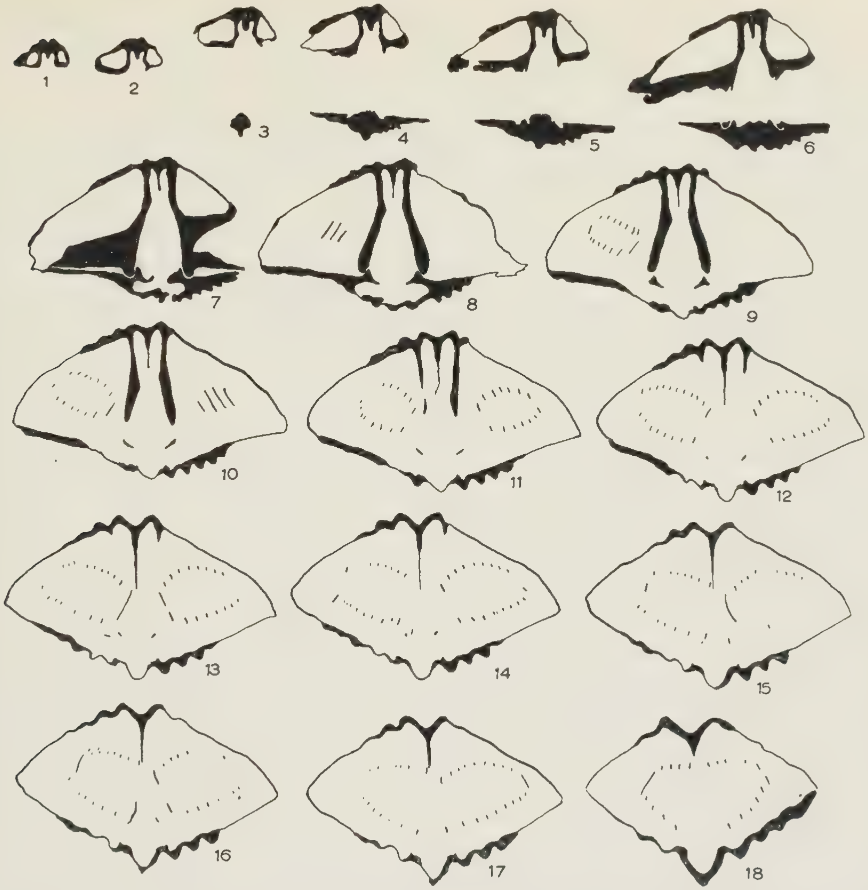
The umbo of the brachial valve is solid. The sockets appear to be rather shallow until the adult stage is reached when they broaden out and become bulbous. In some specimens they encroach on the crural plates. The socket plates arise as strong rounded ridges from the wall of the shell, and they fade out laterally in front of the hinge. The crural plates are welded into the umbonal complex and are not supported on adminicula. Their inner faces are strongly concave. Arising between the crural plates is a broad cardinal process. The postero-dorsal edges of the crural plates give the impression of being tucked in behind the cardinal process. The anterior face of the cardinal process is smooth towards the base, but ventrally it begins to become furrowed and its postero-ventral face is deeply divided into about twenty platelets. Encroaching on to the base of the cardinal process and the inner edges of the crural plates there may be a layer of shell tissue connected with the outer wall. The crural plates and process themselves are formed of impunctate tissue and this investing material can be easily detected since it is punctate.



TEXT-FIG. 2. Serial sections of a specimen of *Punctospirifer scabricosta* North. The interval between sections 9 and 10 is 0·02 inch; the remainder are 0·01 inch. ×2. BB. 20431, B.M.

Dividing the muscle field is a very weak median ridge which is continuous into the umbonal thickening. The central pair of adductors are very long. In adults they have their posterior edge *c.* 2·5 to 3 mm. forward of the umbo. They vary considerably in length and in width. In one of the three specimens where they are well exposed they reach a length of 6 mm. (total length of valve 11 mm.) though in the other two they are relatively shorter—4·5 mm. and 5 mm. in total lengths of 11 mm. each. The central scars spread out on to the furrows bordering the fold and even, occasionally, encroach on the first lateral plica. Posteriorly they are slightly depressed, and laterally they are bounded by clear-cut ridges which fade away almost completely to the front. These lateral bounding ridges extend backwards almost to the crural plates as bases for the attachment of the outer edges of the postero-lateral adductors.

The spires are directed postero-laterally and in adults there are *c.* twelve volutions in each spire. In none of the five specimens I have sectioned is there any sign of a jugum, and since the spires in two of these specimens are still more or less in position, I believe



TEXT-FIG. 3. Serial sections of a specimen of *Punctospirifer scabricosta* North. The intervals between sections 1 and 2, and 7 to 13, are 0·02 inch; between 17 and 18 it is 0·06 inch; the remainder are 0·01 inch. × 1½. 64284 Garwood Collection, G.S.M.

that, at least in these, a jugum was never present. There do not appear to be any spines on the spires.

Remarks. North gives the number of plicae on the lateral slopes as seven to ten, but almost every specimen I have examined has either eight or nine. The structure of the jugum remains a problem. North (p. 213) records that it is 'slender, and forms a shallow V-shaped process, with its apex directed ventrally and posteriorly'. Stehli (1954) states that this is probably erroneous and that the jugum in certain specimens he has examined is anteriorly directed, but he does not make it clear whether or not his observations are on topotypes. My own observations indicate that the jugum was not always developed.

The fine radial ornament on the holotype appears to be less regularly developed than in the figured topotype, and the radial threads are not continuous from lamella to lamella but rather increase in size on each lamella from back to front. Well-preserved specimens always show the arrangement of the figured topotype, and there is little doubt that the condition of the holotype is due to slight wear.

Reticulariina spinosa (Norwood and Pratten)

Plate 59, figs. 10–14; Plate 60, figs. 4, 5

Material. Five specimens in the Davidson Collection at the British Museum, from the Mississippian Chester Limestone, Chester, Illinois, and bearing a label 'given to me by Mr. Worthen'. Twenty-five specimens from the Illinois Geol. Surv. Coll., also collected by Amos Worthen, from the same locality.

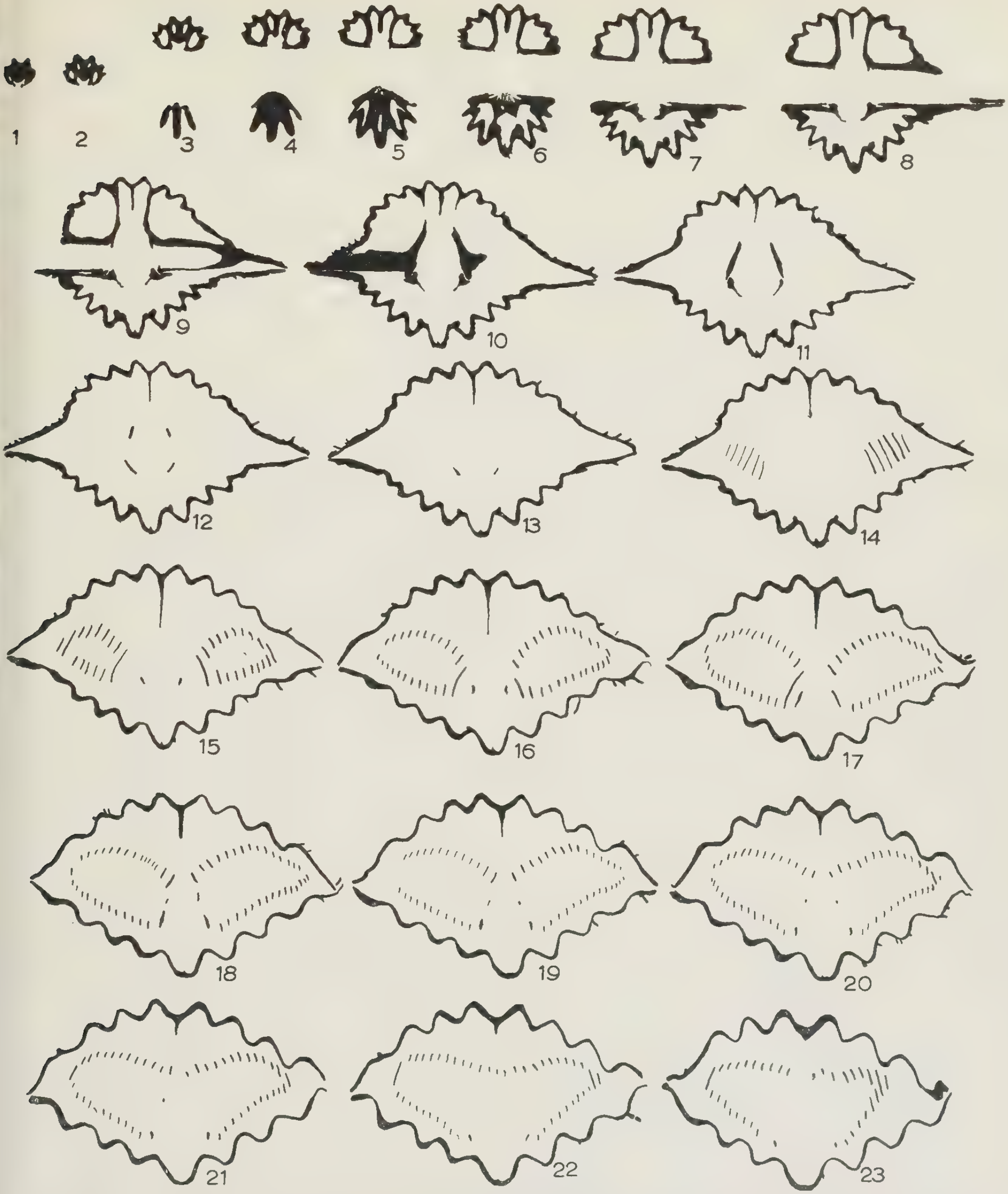
Description. This species reaches a large size for a Palaeozoic punctate spirifer. The outline is invariably transverse, the length being about three-fifths of the width.

The cardinal area of the pedicle valve is low and rather strongly concave, and the umbo does not project far behind the hinge. The delthyrial angle averages 45°. At all stages of ontogeny the cardinal extremities are rounded, except in an occasional specimen in which they tend to be sub-rectangular or even slightly acute. There is no evidence that the shape of the extremities changes during ontogeny. The sinus is usually well rounded and the sinal angle averages 22°. There are five plicae on each of the lateral slopes, and occasional traces of a sixth. In section the plicae tend to be flat sided and well rounded on the crest.

In lateral profile the brachial valve is highly arched. The fold is well rounded overall, but carries a very faint median depression in most specimens.

The superficial shell layer is very thin and shows extremely fine growth lines, spaced *c.* 15–20 per mm. There is no sign of lamellation or imbrication such as occurs in the other punctate genera, but only occasional growth halts which become more numerous toward the front of the shell. The surface also carries a large number of tubular spines which reach a far greater size than those of any other described punctate spirifer. In general the spines are largest on the crests of the plicae and decrease in size on their flanks. They are generally absent from the base of the inter-plical furrows, though occasionally an isolated one is found. On the axial region of the sinus the spines are enlarged. Towards the umbo they are arranged in a single irregular zigzag row, but towards the front they have no clear-cut pattern. On the brachial valve the pattern of spine arrangement is similar to that of the pedicle, except that large spines of the same size as those on the crests of the plicae occur on the crest of the fold, while those on its flanks are of a lesser size. All spines are set at a low angle to the shell surface and are radially disposed with respect to the umbo. Because of this, they leave an elliptical scar where they break off. Scars with a long axis of 0·4 mm. are not uncommon, while the smaller ones are often down to 0·1 mm. In external diameter the spines are up to 0·3 mm. at their base, but most are smaller. They taper very gradually. Their length is not definitely known, but fragments up to 1·5 mm. have been observed. They seem to be formed from the outer shell layer, the inner one being extremely thin, if it is present at all. The spines were occupied by mantle tissue only whilst they were at the growing edge. Subsequently they were sealed off by the normal punctate secondary shell layer.

The cardinal area of the pedicle valve is subdivided into broad, almost smooth, portions on either side of the delthyrium and narrow subtriangular spine-bearing portions against the cardinal ridges. There is a sharp, slightly raised line of division between the two regions. The inner portions are smooth except for faint growth lines and weak, irregular transverse striae. These latter are not denticle grooves—denticles are never developed. The spines on the outer portions show no clear-cut pattern. They are



TEXT-FIG. 4. Serial sections of a specimen of *Reticulariina spinosa* (Norwood and Pratten). The intervals between sections 14 to 17, and 22 to 23, are all 0·02 inch; the remainder are 0·01 inch. ×2. S 16225, S.M.

rather smaller than the average for spines on the body of the shell and are set at a high angle to the surface of the cardinal area. Their average diameter at their base is 0·1 mm. with a range of 0·05 to 0·15 mm. The cardinal area of the brachial valve is similarly subdivided, though the spinose region is so narrow that it is imperceptible on most specimens.

The punctae of the secondary layer either stop short at the primary layer, or they just penetrate its base. So far as I am able to determine, wherever the primary layer is undisturbed the punctae fail to reach the surface of the shell. Their diameter is 0·06 to 0·1 mm., most being approximately 0·075 mm., and they are spaced 75 to 100 per sq. mm. On the cardinal area they are somewhat finer and slightly more closely spaced.

Interior. The callus in the tip of the umbo is very small and results in the septum being united with the inner faces of the adminicula. The septum is as shown in text-fig. 6. It is a slender structure with secondary deposition on its sides as in *P. scabricosta*, and it reaches approximately half the length of the shell. The dental lamellae and adminicula are moderately thick, the latter reaching about one-third the length of the shell and run along the furrows immediately lateral to the sinus. The diductor insertions are not known.

The cardinal process is a small recessive structure situated on a very low umbonal callus. The crural plates are broad and concave on their inner faces with their inner edges sharply inflected. The descending lamellae are straight and sub-parallel to the jugum, but forward from that structure they diverge and swing away dorsally. The jugum, in the only specimen in which it has been observed, consists of a pair of prongs directed antero-ventrally and slightly inwards toward the median plane. They do not appear to meet. There are *c.* sixteen volutions in the spires of adults. A weak median keel divides the adductor scars which reach *c.* half the length of the valve. The ridges on the outer edges of the postero-lateral adductor scars are strong, rounded, and rise abruptly from the shell wall. They are situated on the outer side of the crest of the furrow bordering the fold.

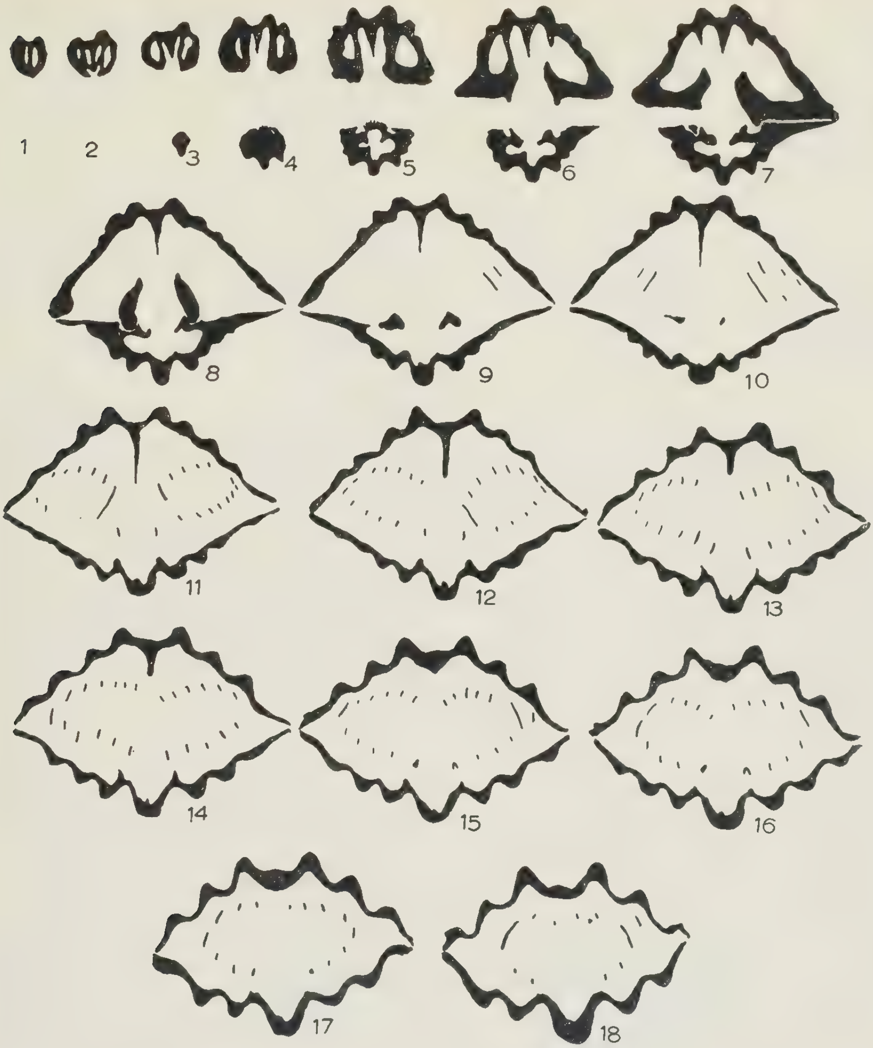
Remarks. This description differs from the original of Norwood and Pratten in a number of points. The growth lines (striae of N. and P.) are not imbricate except towards the front of occasional specimens; the spines are never at right angles to the shell surface (except on the cardinal area); and the 'minute granules' which were reputed to cover the whole shell are in fact the ends of the infillings of the punctae, which project slightly when the surface layers of the shell have been removed.

The large spines, non-lamellose shell, and relatively small boss for the cardinal process permit the rapid discrimination of this species. It is possible that the jugum is complete in some specimens, but I have not observed this in my material.

Spiriferellina cristata (Schlotheim)

Plate 59, figs. 1–9; Plate 60, fig. 3

Material. Lectotype (here chosen) B.-K. Sp. 33.1 collection of the Geologisch-Paläontologisches Institut und Museum, Berlin: from the Zechstein of Glücksbrunnen, Thüringen. The remainder of Schlotheim's syntypes are in the same institution, numbers B.-K. Sp. 33.2 to B.-K. Sp. 33.12. In addition 5 topotypes in the Sedgwick Museum and about 20 specimens from Pössneck, Thuringia, in the British Museum, have been examined.



TEXT-FIG. 5. Serial sections of a specimen of *Spiriferellina cristata* (Schlotheim). The intervals between sections 10 and 11, and 16 and 17, are 0·02 inch; the remainder are 0·01 inch. ×3. BB 20430, B.M.

Description of type specimens. Most of the specimens are in a poor state of preservation and many are fragmentary.

The shell is small, the largest having a maximum width of *c.* 14 mm. The pedicle umbo is rather high and pointed and curved over the cardinal area at its tip. Throughout ontogeny the cardinal extremities are well rounded, and hence the lateral slopes curve around on to a subdued, more or less rounded cardinal ridge. The plicae are high and subangular and usually number four on each side of the sinus, with an incipient fifth. In all specimens the sides of the sinus are steep and the floor flat, the junction between the two being quite angular. In the largest specimens the floor tends to be slightly domed towards the front. The fold and sinus have the appearance of being of the same order of magnitude as the bounding plicae.

The cardinal area meets the hinge almost at right angles to the plane of the commissure, and its concavity is very slight except toward the umbo where it increases abruptly. There are traces of transverse striae on the area, but there are no signs of denticles or denticle grooves.

The brachial valve has a prominent little umbo and a strongly concave area. The fold is rather sharp with a rather rounded crest at the juvenile stage. No adult folds are preserved.

The surface lamellae are very variably arranged. On some juveniles they are rather

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EXPLANATION OF PLATE 58

All figures are of topotypes, and all × 2.

Figs. 1–10. *Punctospirifer scabricosta* North. 1*a–e*, Ventral, dorsal, posterior, anterior, and lateral views, E 10405 S.M. 2*a–d*, Ventral, dorsal, posterior, and anterior views, E 10403 S.M. 3*a–e*, Ventral, dorsal, posterior, anterior, and lateral views, E 10404 S.M. 4*a–e*, Same, E 10402 S.M. 5*a–d*, Ventral, dorsal, posterior, and anterior views, JGG 1260 G.S.M. 6*a–d*, Ventral, posterior, anterior, and lateral views, E 10406 S.M. 7*a–b*, Interior of a brachial valve, and rubber mould of same. The blemish on the infilling of the socket on the right of the specimen is due to faulty casting. E 10422 S.M. 8*a–b*, Same, E 10421 S.M. 9, Interior of a brachial valve, E 10420 S.M. Note the differing forms of the cardinal process in these three specimens. 10, Prepared section of a complete specimen cut through the two umbones and down one dental lamella and adminicula. Note the small callus in the pedicle umbo, the ridges on the inner face of the dental lamella, the dental ridge, and the descending lamella of the spire, E 10407 S.M.

EXPLANATION OF PLATE 59

All figures × 2.

Figs. 1–9. *Spiriferellina cristata* (Schlotheim). 1*a–c*, Dorsal, anterior, and posterior views of a syntype, B.K. Sp. 33.2 H.U.B. 2*a–e*, Ventral, dorsal, anterior, posterior, and lateral views, BB. 20432 B.M. 3*a–d*, Ventral, dorsal, anterior, and lateral views, BB. 20435 B.M. 4*a–d*, Ventral, dorsal, anterior, and posterior views, BB. 20434 B.M. 5*a–c*, Ventral, dorsal, and anterior views of a syntype, B.K. Sp. 33.3 H.U.B. 6*a–b*, Dorsal and anterior views, BB. 20433. 7*a–b*, Ventral and posterior views of the lectotype. 8, Internal view of a broken specimen showing the spires, BB. 20440 B.M. 9, Same showing spires, end of the ventral septum, and the incomplete jugum, BB. 20441 B.M. Specimens 2–4, 6, 8–9 from Pössneck.

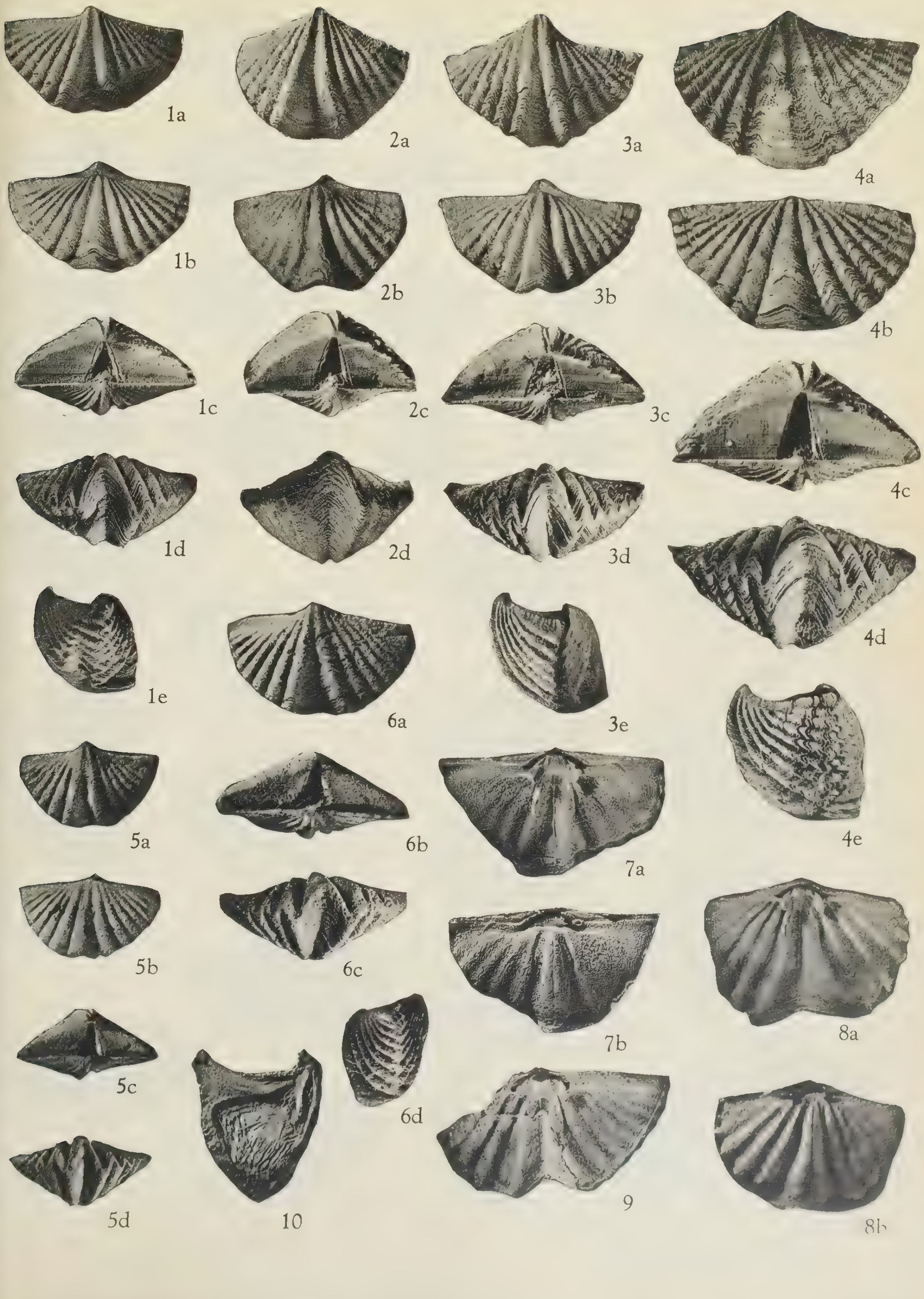
Figs. 10–15. *Reticulariina spinosa* (Norwood and Pratten). 10*a–d*, Ventral, dorsal, anterior, and lateral views of a large specimen, BB. 7930 B.M. 11*a–e*, Ventral, dorsal, anterior, posterior, and lateral views, BB. 20436 B.M. Note the spines on the cardinal area of 11*d*. 12*a–d*, Ventral, dorsal, lateral, and posterior views, BB. 20437 B.M. 13*a–b*, Ventral and dorsal views, BB. 20439 B.M. 14, Interior of a brachial valve, E 16227 S.M. Note the sharp inflection of the inner edges of the crural plates. 15*a–c*, Ventral, dorsal, and posterior views, BB. 20438 B.M. Note the position of the ventral adminicula and the crural plates in 15*c*. All specimens from Chester, Illinois.

EXPLANATION OF PLATE 60

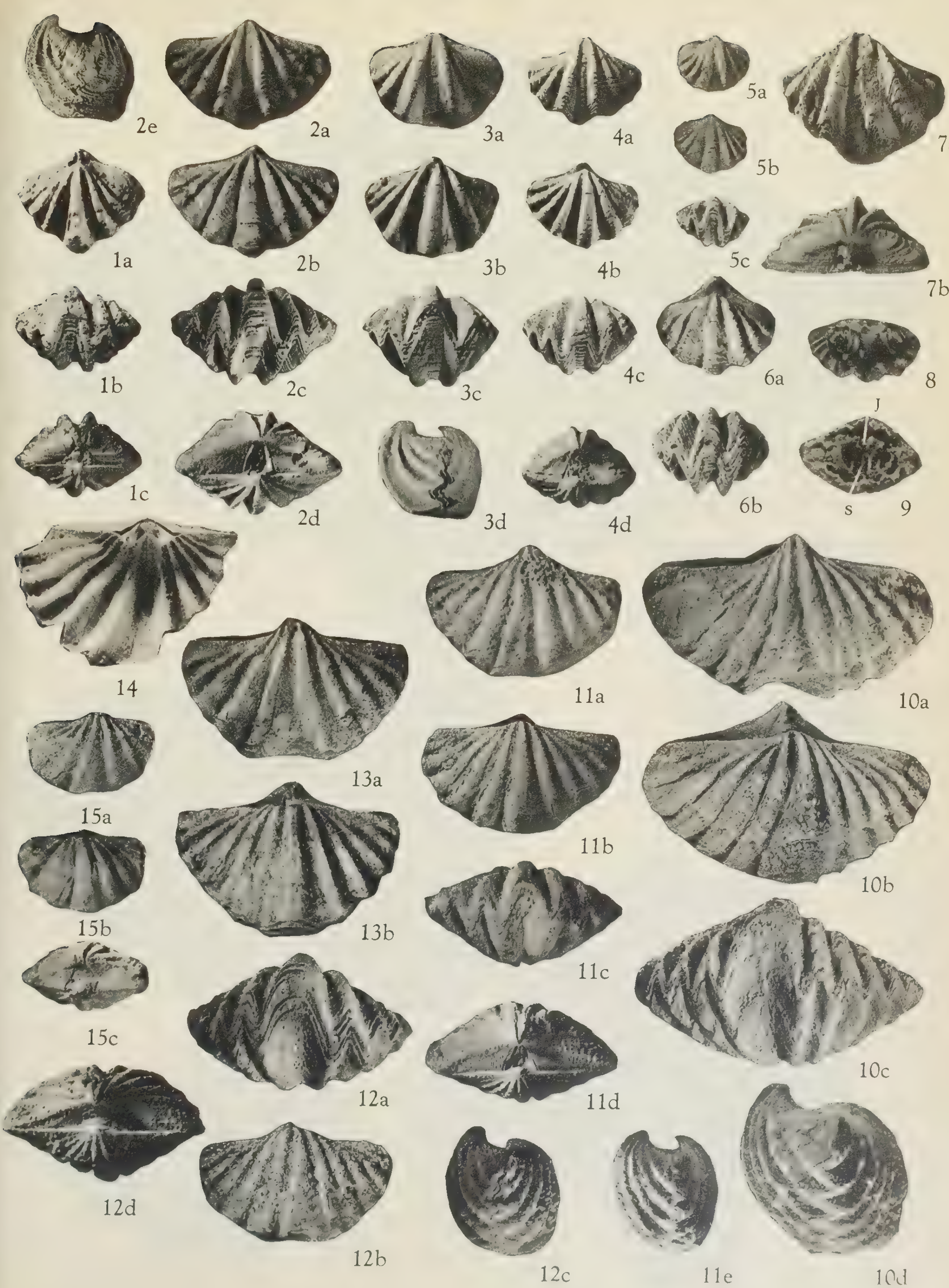
Figs. 1, 2. *Punctospirifer scabricosta* North. 1, Ventral view of E 10402 S.M. The cellular structure on the centre of the specimen is a bryozoan, × 7·2. 2, Part of the sinus of the holotype, × 8.

Fig. 3. *Spiriferellina cristata* (Schlotheim). Ventral view of lectotype, × 7·2.

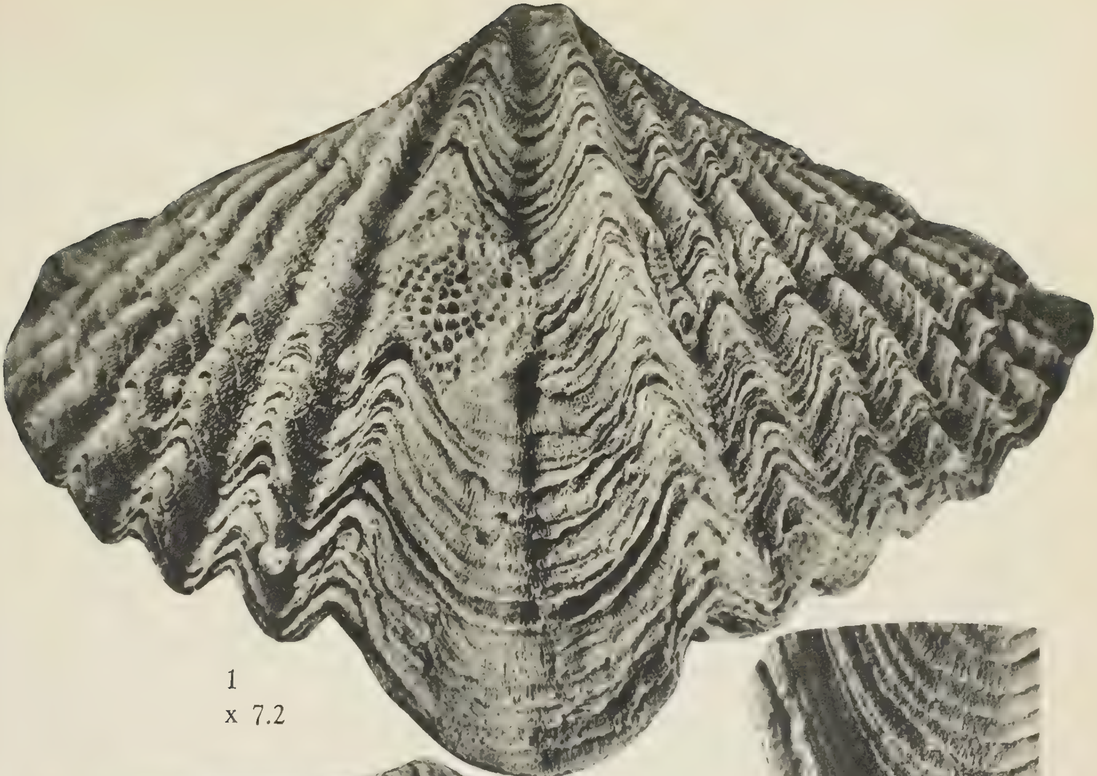
Figs. 4, 5. *Reticulariina spinosa* (Norwood and Pratten). 4, Part of the brachial valve of a specimen from Chester showing the spines and the ends of the infillings of the punctae, BB. 20437 B.M., × 7·2. 5, Ventral view of a specimen from Chester, showing the arrangement of the spines, E 16226 S.M., × 3·2.



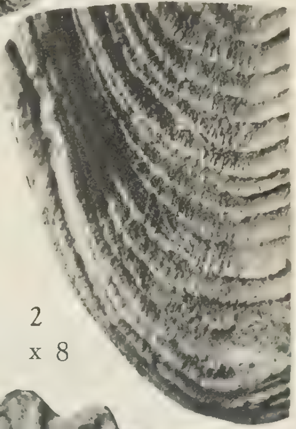
CAMPBELL, *Punctospirifer scabricosta*, all x2



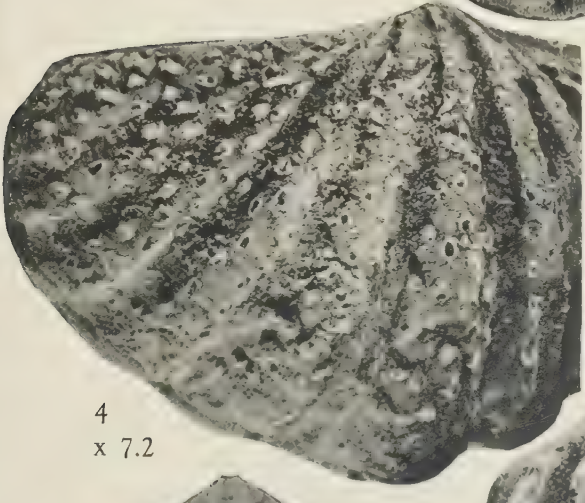
CAMPBELL, *Spiriferellina* and *Reticulariina*



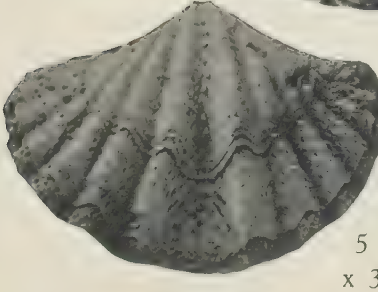
1
x 7.2



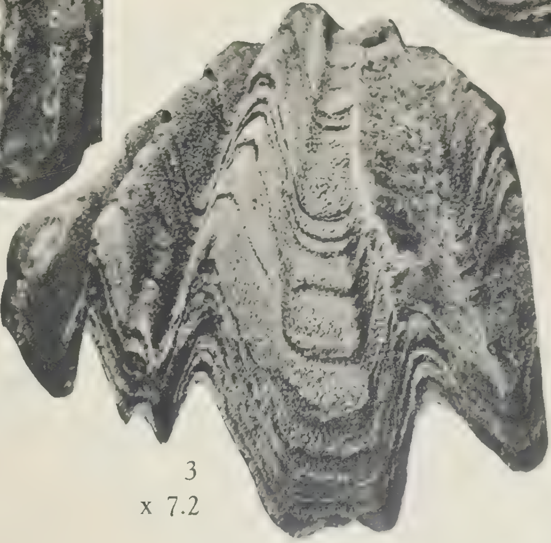
2
x 8



4
x 7.2



5
x 3.2



3
x 7.2

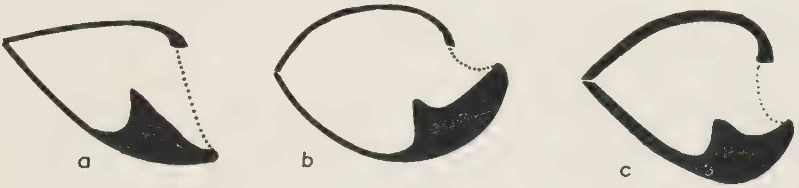
CAMPBELL, Punctate Spiriferoids

regularly and closely spaced, while on others they are few and widely spaced. Towards the anterior margin in adults the lamellae tend to become numerous and imbricate, but on other parts of the shell they are rarely so. The whole surface, except for the cardinal areas, is covered with fine granules which appear to coincide in position with the outer ends of the punctae. Some specimens give the impression that these granules are due to slight decomposition of the surface layer of the shell permitting the ends of the infilled punctae to protrude through, but one specimen, Sp. 33.10, is an external mould which shows the granules to be an original surface feature.

Very little can be learned of the internal structures save that there are dental lamellae, adminicula, and a median septum in the pedicle valve, and a median keel of unknown length in the brachial. The ventral adminicula are very short and extend down the furrow lateral to the sinus. The septum is much longer than the adminicula.

Other specimens. The British Museum has a number of specimens from the Zechstein dolomite at Pössneck, Thuringia, the same horizon as that from which the types come. The preservation of the specimens is excellent, and so far as one can judge from the imperfect types, the two groups are conspecific. The following additional features are exhibited by the Pössneck specimens:

There is a considerable range in the variation of L/W ratios. The relatively broader forms have one more plication on the lateral slopes (i.e. five instead of four). There is also considerable variation in the number and spacing of the lamellae. The fold tends to become quite flattened on the crest during ontogeny. The fine granulation of the surface appears to be due to the development of extremely small nodes on the surface over the ends of the punctae. These nodes can be clearly seen at a magnification of 4 or 5. They are entire, and are clearly not the bases of spinules. They are irregularly spaced at 80 to 150 per sq. mm. The diameter of the punctae is 0·06 to 0·1 mm.



TEXT-FIG. 6. Median longitudinal sections of (*a*) *P. scabricosta*, 64284*b* G.S.M., (*b*) *R. spinosa* S 1622*b* S.M., and (*c*) *S. cristata*. (*a*) and (*b*) are drawn from actual median sections with slight reconstruction and are ×2. (*c*) is reconstructed from transverse serial sections, and is ×3.

Interior. The median septum of the pedicle valve is very broadly based. It rises gradually and then more rapidly towards the front, following which it is abruptly truncated. Its highest point is *c.* one-third the length of the shell from the umbo. Seen laterally, the dental plates and adminicula are of the same style as in *Punctospirifer*. The adminicula are short (one-quarter the length of the valve), and the dental lamellae are very robust. In the tip of the umbo there is a small callus which does not protrude through the delthyrium. Muscle scars are not known.

The cardinal process is a small platy structure supported on an umbonal boss into which are fused the inner edges of the crural plates. The central pair of adductor scars extend to about the mid-length of the valve and are separated by a weak median ridge.

The postero-lateral adductor scars are bordered by high ridges which assume septum-like proportions in some specimens. They are situated on the outer slope of the depressions bordering the median fold. The spires are non-spinose, are formed of six or seven volutions, and are directed postero-laterally. The descending lamellae are straight and sub-parallel from the crura to the jugum, but beyond that structure they diverge rather sharply. In the only specimen in which the jugum has been observed it is incomplete, perhaps due to fracture. The two arms project slightly forwards and inwards, and then bend abruptly towards each other.

Remarks. The internal structures are known from a few poorly preserved specimens from which the loose matrix has been removed, and from one specimen which has been serially sectioned. The preservation is in carbonate which often has almost the same colour as the shell so that it is difficult to differentiate between shell substance and matrix on many polished surfaces. A further difficulty is introduced by the encrustation of the internal features by a fairly thick layer of carbonate.

One of the best descriptions of *S. cristata* is that by Malzahn (1937), who has also given an extensive synonymy. It is impossible to check the synonymy without examination of the specimens since almost all descriptions omit to mention vital morphological features.

DIMENSIONS (in mm.)

P. scabricosta

Length	*Length brachial valve*	*Width*	*Height*	*Height of fold*	*Distance between tips of the two umbones*
11·5	11	*c.* 21	11·5	4·5	5·5
9·5	8·7	14	10	4	4·2
10	8·5	16·5	9·5	3·5	*c.* 3·5
8·5	8	15	7·5	3	4
		S. cristata			
7·5	6·8	10	8	. .	1·5
8·5	8	13·5	8·5	3	2·8
8	7·5	10·5	8	3	2
7	*c.* 6·5	*c.* 12	7·5	2·5	. .
4·5	4·3	. .	4	1·3	. .
		R. spinosa			
13·5	12	23	13	7	3
12	11	19	10·5	4	. .
9·2	9	16	8·3	3	2
10	9·2	15	9	2·4	2

Acknowledgements. I am indebted to Dr. W. O. Dietrich and Dr. H. Jaeger of the Humboldt Universität, Berlin, for the loan of Schlotheim's types of *Terebratulites cristatus*; Dr. H. M. Muir-Wood of the British Museum (Natural History) for the loan of specimens; Dr. W. H. C. Ramsbottom for the loan of material from the Geological Survey Museum, London, and also for the photograph given as Pl. 60, fig. 2; Professor Kenneth Brill of the University of St. Louis for the gift of specimens of *Reticulariina* *spinosa* from Paint Creek; Dr. Charles Collinson of the Illinois Geological Survey for the gift of topotypes of *R. spinosa*; Dr. M. J. S. Rudwick, Sedgwick Museum, for assistance with the illustrations; Mr. A. Barlow, Sedgwick Museum, for the photographs. The work was carried out at the Sedgwick Museum, Cambridge, during the tenure of a Nuffield Dominion Travelling Fellowship.

Repositories. S.M., Sedgwick Museum, Cambridge. B.M., British Museum (Natural History). H.U.B., Humboldt Universität zu Berlin. G.S.M., Geological Survey and Museum, London.

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Manuscript received 21 July 1958

GEOLOGICAL DISTRIBUTION OF *DISCOSPIRINA* (FORAMINIFERA) AND OCCURRENCE OF *D. ITALICA* IN THE MIOCENE OF CYPRUS

by C. G. ADAMS

ABSTRACT. Previous records of *Cycloloculina miocenica* Cushman and Ponton from the Miocene of Cyprus are shown to be based on misidentifications of *Discospirina italica* (Costa). Examination of existing records of the latter genus indicates that its geological range may now be assumed to be Middle Miocene to Recent.

THE Geological Survey of Cyprus recently submitted a large number of foraminiferal specimens preserved in blocks of fine-grained chalky Miocene limestone, and requested confirmation of their identification of *Cycloloculina miocenica* Cushman and Ponton. Examination revealed that all the specimens were *Discospirina italica* (Costa), and this prompted an investigation of the previously published record (Dusenbury 1949) of *C. miocenica* from Cyprus. It was found that this also was based on a misidentification of *D. italica.* As these foraminifera have been used as marker fossils for the Miocene of the area it seemed desirable to correct the name and to determine, as far as possible, the range of the genus in case it should prove of value in dating Tertiary sediments. This entailed a comprehensive search of the literature and the author is indebted to Miss C. M. Underwood for her assistance with this. His thanks are also due to Dr. A. H. Smout and the management and Chief Geologist of the Iraq Petroleum Company for allowing him to examine some of their material; to Dr. H. W. Ball who read the typescript and to Dr. R. H. Hedley who also read the typescript and kindly took the microradiograph.

Family OPHTHALMIDIIDAE

Genus DISCOSPIRINA Munier-Chalmas 1902

Type species by monotypy *Orbitolites tenuissimus* Carpenter, a subjective synonym of *Pavonina italica* Costa

1903 *Cyclophthalmidium* Lister, p. 110 (type species *O. tenuissimus* Carpenter).
1920 *Krumbachina* Wiesner, p. 14 (type species *O. tenuissimus* Carpenter).

Remarks. Authors subsequent to Munier-Chalmas have sometimes included *D. italica* as a separate species, and sometimes regarded *D. italica* and *D. tenuissima* as synonymous.

Discospirina italica (Costa)

Plate 61

1856 *Pavonina italica* Costa, p. 178, pl. 16, figs. 26–28.
1870 *Orbitolites tenuissimus* Carpenter, p. 8.
1883 *Orbitolites tenuissima* Carpenter, pp. 553–9, pl. 37–38.
1886 *Orbitolites italica* (Costa), Brady, p. 191.
1932 *Orbitolites tenuissima* Carpenter, Lipparini, pp. 8, 18.
1949 *Cycloloculina miocenica* Cushman and Ponton, Dusenbury *in* Henson, Browne, and McGinty, pp. 21, 24, 25.

[Palaeontology, Vol. 1, Part 4, 1959, pp. 364–8, pl. 61.]

Apart from the type references of Carpenter, only the fossil records of the genus are included here. A more complete list of recent records and references can be obtained from Ellis and Messina (1940 et seq.) under 'Additional References for *O. tenuissimus* Carpenter'.

Material and localities. Over 100 specimens from the Upper Pakhna siliceous marls of Cyprus, British Museum (Natural History) P. 43936–8. Thirteen specimens from the 'Miocene (Dhali formation) St. Theodore, Cyprus', the property of the Iraq Petroleum Co., Ltd., London. Two specimens from Castanea, near Messina, Sicily, Ex. H. B. Brady Collection, British Museum (Natural History) P. 43934.

Description. The compressed, calcareous imperforate test consists of an initial coil of chambers arranged in an Ophthalmidium-like manner, followed by a number of uncoiling chambers which gradually expand laterally until they become annular and enclose the initial coil. The adult test is therefore disk-shaped. Three stages in test growth can be recognized.

1. An initial coil in which the chambers make up to five or more turns round the globular proloculum, individual chambers being $\frac{1}{2}$–$1\frac{1}{4}$ turns in length.
2. An uncoiling stage in which the chambers increase rapidly in size and begin to develop septa.
3. A final stage commencing with the growth of semi-annular chambers and ending with the development of completely annular chambers.

In the second and third stages the chambers are characterized by the presence of numerous internal septa which stop short of the anterior border of each chamber. The diameter of the test is usually 5 to 6 mm.; maximum diameter recorded 7 mm.

Remarks. W. B. Carpenter (1870, 1883*a*) has given detailed descriptions of the living representatives of the genus to which nothing can be added here. The Miocene specimens appear to differ from the living ones mainly in size. Whereas the latter range up to 20 mm. (Flint 1899, p. 305) or even 30 mm. (Lister 1903, p. 108) in diameter, the former are not known to exceed 7 mm. It should be noted that Lister does not figure or describe these very large specimens, nor does he say where they were found. The diameter of the largest recent specimen in the British Museum Collection is 13·5 mm. Carpenter (op. cit.) estimated that the maximum diameter of the tests he examined was 0·6 inch (= 16 mm.). Exact measurements are rarely possible as the largest tests, which are very fragile, have always been obtained in a broken condition. The large size of the modern tests appears to be due to an increase in the number of annular, i.e. third stage, chambers, and not to a difference in the rate or pattern of growth. It has been noticed that there are more septa per annular chamber in the recent than in the fossil specimens. Further work on better-preserved fossil material and on additional Recent material might indicate that this is a character of specific importance, in which case a new name will be required for the Miocene forms. The diameter of the initial coil is not appreciably greater in the living forms than in the fossils, neither is the number or size of the chambers in the second stage in any way different. For these reasons the author considers that all the known representatives of *Discospirina* should be included for the present under one specific name. Another argument in favour of this is that no practical stratigraphic advantage results from regarding them as two species.

It is unfortunate that the excellent description and figures of Carpenter should have been pre-dated by the relatively poor ones of Costa. However, despite the small size of Costa's specimen (max. diam. 2·8 mm.) and the fact that the details of the initial coil cannot be seen, although the outline can, there is no doubt that he was figuring the same organism. There are two reasons for stating this: (1) No known foraminifera, other than *Discospirina*, have a structure closely resembling that depicted by Costa. (2) Good specimens of *Discospirina*, larger than Costa's and similar to Carpenter's, except in size, are now known from the Miocene of Sicily and Italy. It is therefore probable that the same species existed there during the Pliocene.

In the annual report of the Geological Survey of Cyprus for 1956, there is (p. 35) a reference to specimens which 'greatly resemble *Cycloloculina*'. This is certainly a misidentification of *Discospirina*, and the 'coarse perforations' reported are no doubt caused by the septa showing through the thin wall of the test. This pseudo-perforate appearance is quite common.

Geological distribution. The range of the genus has been given as Pliocene to Recent (Galloway 1933), late Tertiary to Recent (Glaessner 1945), Tertiary and Recent (Cushman 1927, 1928, and subsequent editions to 1940), and Upper Cretaceous to Recent (Cushman 1948). This last statement is probably a printing error as Cushman cites no evidence for the change and states elsewhere in the same edition (p. 188) that *Discospirina* is known only 'from the present oceans or late Tertiary'. Sigal (1952) also gives the range as Upper Cretaceous to Recent but this appears to be a copy of the error in the last edition of Cushman. Carpenter (1883*a*, p. 559; 1883*b*, p. 20) expressed the opinion that *Orbitolites tenuissima* was an early form of the genus which probably existed throughout the greater part of the Tertiary. But since Carpenter, who believed in Orthogenesis and regarded the initial coil as a primitive feature, had placed his species in the wrong genus, no importance need now be attached to his view. The only known fossil record at the time Carpenter wrote was *Pavonina italica* Costa from the Pliocene of Italy, and he did express the view (1883*a*, p. 559) that the two species might be identical.

Brady (1886) stated that although he had been unable to obtain any information about Costa's figures from Professor Seguenza of Messina, he had been furnished with some friable Upper Miocene limestone containing *O. italica*. These specimens are now in the British Museum (Natural History), number P. 43934, and are clearly *Discospirina*; this constitutes the first record of the genus from any rock older than the Pliocene. The diameter of these specimens is 6 and 7 mm. respectively. There appears to be no further record until Lipparini (1932) found it in the Upper Miocene, 'Marne Azzure', near Bologna. Lipparini (p. 18) gave the previous range of the species as Pliocene to Recent

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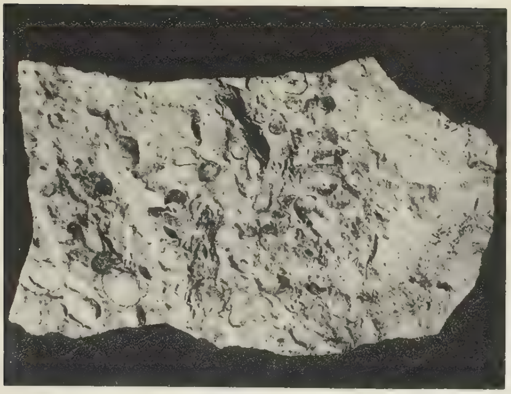
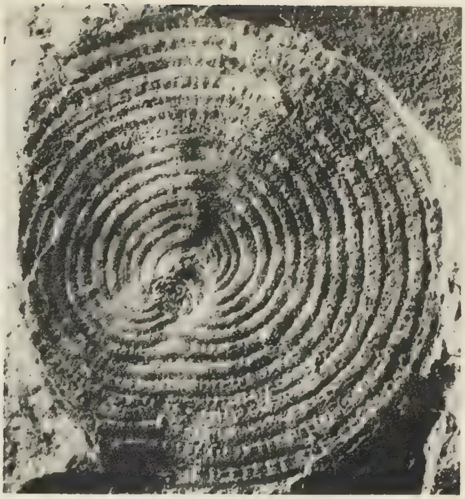
EXPLANATION OF PLATE 61

The specimens are in the British Museum (Natural History).

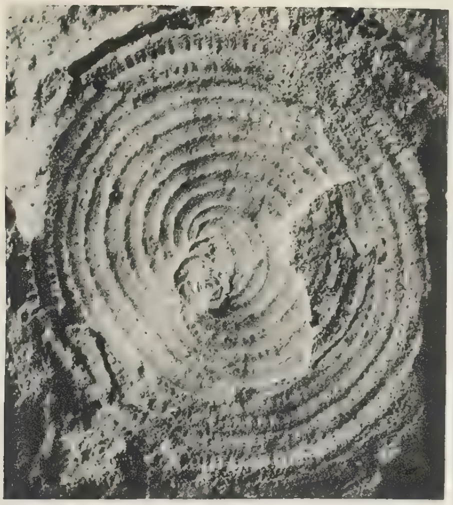
Figs. 1–6. *Discospirina italica* (Costa). 1, Block of Miocene limestone from Cyprus showing the surface crowded with *Discospirina*; P. 43936. 2, Well-developed specimen showing septa in the annular chambers; Miocene, Cyprus, P. 43936. 3, Showing septa in second and third stages; Miocene, Cyprus, P. 43936. 4, Enlargement of same specimen as fig. 3 to show structure of first and second stages. 5, Recent specimen, off north-west coast of Africa, 28° 25′ N., 13° 34′ W., depth 1,300 m.; 1958. 3. 41. 6, Direct print of X-ray photograph of the same specimen as fig. 5 to show internal structure. Radiographic factors: 25 kv, 10 mA, 15 cm., 15 mins.



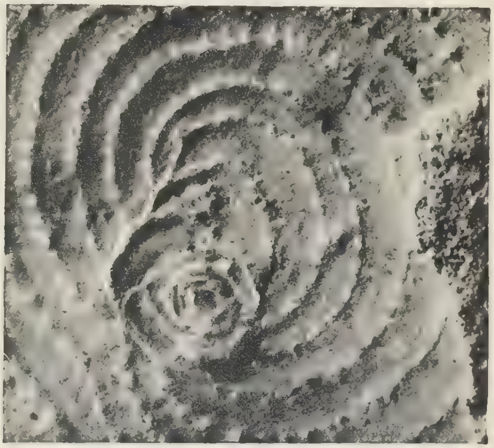
1 3 *cm.*



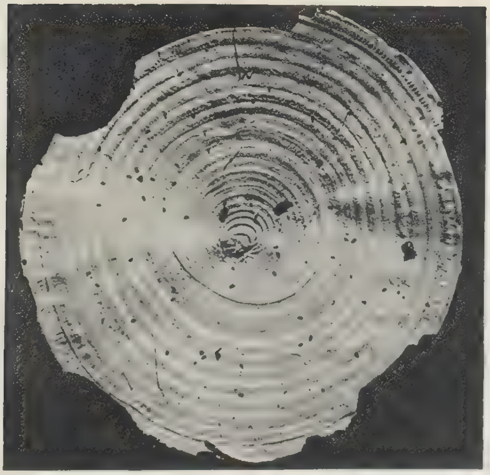
2 3 *mm.*



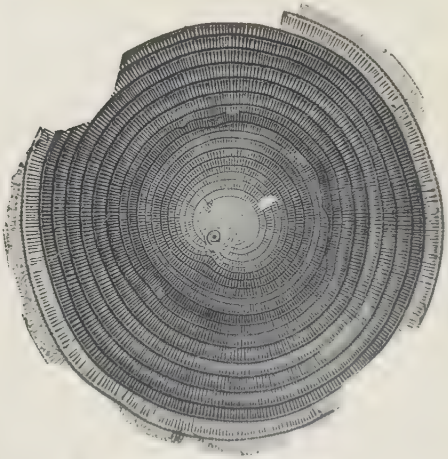
3 3 *mm.*



4 1 *mm.*



5 6 *mm.*



6 6 *mm.*

ADAMS, *Discospirina italica*

and indicated that it should be extended back to the Miocene; he was apparently unaware of Brady's paper. The author knows of no other record until that of Dusenbury (1949). This, as has been shown, was a misidentification which was subsequently accepted and perpetuated by the geologists of the Cyprus Geological Survey.

There are many records of living representatives of the genus from the North Atlantic and Mediterranean, for details see Carpenter (1883*a*, *b*) and Brady (1884). It lives in both cool, deep water and warm, shallow water.

The available evidence suggests that *Discospirina* appeared in the Mediterranean area during the Upper Miocene and has continued to live there until today. Statements that it existed, or may have existed, in early Tertiary times cannot be substantiated, and the following negative evidence is also opposed to this view: (1) Wherever *Discospirina* is found fossil it seems to occur in large numbers; it is typically preserved in fine-grained chalky limestones or clays. Limestones of an apparently suitable lithological type occur as a thick succession from Upper Cretaceous to Oligocene or Lower Miocene (the Lapithos Group) in Cyprus. *Discospirina* has not, however, been found in this succession, and it is very unlikely that such distinctive and large foraminifera could have been missed. (2) During the last thirty years a great deal of micropalaeontological research has been carried out on the lower Tertiary successions of the Mediterranean area, and so far as the author has been able to ascertain, no record of the genus has been published. The probability is therefore great that it did not appear in the area until Middle Miocene times.

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ASHGILLIAN TRILOBITES FROM CO. CLARE, IRELAND

by J. A. WEIR

ABSTRACT. Fifteen species are described and figured, including *Corrugatagnostus convergens* sp. nov., *Shumardia extensa* sp. nov., *Phylacops bituberculatus* sp. nov., and *Dindymene ovalis* sp. nov.; *Thomondia globosa* Harper is redescribed from additional material and assigned to the Family Isocolidae. The trilobites were collected from a thin band in the brown mudstone horizon constituting the lower part of the Ballyvorgal Group, a new division at the top of the Ordovician succession in the Slieve Bernagh Mountains. The fauna has close affinities with that of the Upper Whitehouse Beds (Ashgillian) of the Girvan district, Scotland, and appears to be largely of Bohemian origin.

INTRODUCTION

THIS paper is a systematic description of a trilobite fauna first discovered by Kinahan in brown mudstones cropping out in the stream forming the south-eastern boundary of the townland of Ballyvorgal South, at the south-western end of the Slieve Bernagh Mountains, 2¾ miles north-east of the village of Sixmilebridge, Co. Clare. It is proposed that these mudstones, and the overlying brown shales, be termed the Ballyvorgal Group. Baily (*in* Foot and Kinahan 1862, p. 10) gave a short account of the fauna, recognizing its Bohemian affinities, and in 1885 published another short note. In 1939 Stubblefield (p. 61) noted the affinities of the fauna with that of the Upper Whitehouse Beds of the Girvan district; in that year also, Harper (*in* Smyth and others, p. 303) reported the occurrence of the zonal graptolite *Dicellograptus complanatus* a foot below the trilobite bed. Harper (1942) described a new trilobite genus *Thomondia* from the locality and added *Agnostus perrugatus* to Baily's fossil list. Baily's material is no longer available for study but Stubblefield (1939) interpreted Baily's (1862) illustration of *Olenus?* as being of Barrande's genus *Bohemilla*, an opinion upheld by Harper (*in* Smyth and others 1939) and by Whittard (1952).

The material on which this paper is based was collected by the writer in the course of a revision of the Lower Palaeozoic geology of the area, for which he wishes to acknowledge receipt of a Maintenance Grant from the Department of Scientific and Industrial Research. The writer also wishes to thank the Director of the Geological Survey of Ireland for access to field maps and for the loan of specimens; the British Museum (Natural History) and the Geological Survey of Great Britain for access to fossil collections; also Professor A. Williams, Professor H. B. Whittington, and Mr. R. P. Tripp for guidance, and especially Professor Williams and Mr. Tripp for criticizing the manuscript.

The terminology used is that used in the forthcoming trilobite part of the *Treatise on Invertebrate Paleontology*, which is based on that used by Warburg (1925, p. 7); where possible, dimensions refer to external moulds, although internal moulds are generally more complete and then have to be employed. The type and figured specimens have been presented to the British Museum (Natural History).

[Palaeontology, Vol. 1, Part 4, 1959, pp. 369–83, pls. 62–63]

SYSTEMATIC ACCOUNT

Family AGNOSTIDAE Hawle and Corda 1847

Genus CORRUGATAGNOSTUS Kobayashi 1939

Corrugatagnostus convergens sp. nov.

Plate 62, figs. 17–19

1862 *Olenus?* Baily, p. 10, fig. 1*a*.
1939 *Agnostus* cf. *perrugatus* Harper (*in* Smyth and others), p. 303.
1942 *Agnostus* cf. *perrugatus* Harper, p. 276.

Material. Holotype: B.M. In. 53367 (cephalon), Pl. 62, fig. 19; dimensions of holotype: length of cephalon 3·2 mm., breadth of cephalon 3·4 mm., length of glabella 2·4 mm. Paratypes: B.M. In. 53368 (pygidium), Pl. 62, fig. 17; B.M. In. 53369 (cephalon), Pl. 62, fig. 18. Other material: 5 cephala, 2 pygidia.

Horizon and locality. Ballyvorgal Group (Ashgillian), Ballyvorgal South, Co. Clare, Ireland.

Diagnosis. Corrugatagnostus with median furrow on preglabellar field reaching anterior border, flanked by two converging furrows not reaching border. Anterior and middle glabellar lobes bearing elongate median ridges.

Description. Cephalon moderately convex, nearly square in outline, anterior margin smoothly rounded. Glabella two-thirds the cephalic length, axial furrows strongly impressed, preglabellar furrow less strong; divided into three lobes, the two anterior of equal length and together occupying half the glabellar length; basal lateral lobes large and triangular. Lateral glabellar furrows incomplete, chevron-shaped, deeply impressed. Middle and posterior glabellar lobes produced forwards in axial line to form ridges lying on lobe in front, that on anterior lobe half length of lobe, that on middle lobe extending full length of lobe. Cheeks moderately convex, uniting in front of glabella in broad preglabellar field and bearing shallow radial furrows extending inwards from border furrows, alternate furrows reaching glabella; several furrows bifurcate near border. Median furrow becoming weaker anteriorly, reaching anterior border; two adjacent furrows converging and dying out before reaching anterior border furrow. Borders strongly convex, nearly horizontal, border furrows strongly impressed.

Pygidium gently convex, almost square, posterior margin rounded. Axis nearly flat, half the pygidial length, margins bent down steeply; divided into two equal parts by second ring furrow. Anterior part tapering posteriorly, consisting of two rings, each bearing a narrow median ridge. Posterior part consisting of a simple ring squarely terminated by broad and deep axial furrow. Pleural regions bearing radial furrows, more anastomosing than those on cephalic cheek lobes. Border furrows shallow. Borders broad, smooth, gently convex, nearly horizontal, produced into a pair of short triangular spines at posterior angles. Thorax unknown.

Remarks. The cephalon appears to represent a type intermediate between *Corrugatagnostus morea* (Salter) from the Dγ^1 beds (Llanvirn-Llandeilo) of Bohemia (Whittard 1956, p. 12, text-fig. 2*b*), in which the three median furrows on the preglabellar field converge and do not reach the anterior border furrow, and *C. sol* Whittard from the Upper Whitehouse Group (Ashgillian) of Girvan (1956, pl. 1, fig. 12; Reed 1904, pl. 1, fig. 5) in which the furrows are parallel and reach the anterior border furrow. The two posterior glabellar lobes are extended forwards into discrete median ridges as in *C. morea*, but the ridges are of much greater length than in that species. The pygidium is squarer in outline than in either *C. morea* or *C. sol*, the axis is relatively broader and the posterior lobe more square in outline.

Genus TRINODUS M'Coy 1846

Trinodus? sp.

Plate 63, fig. 9

One incomplete cephalon may be referable to this genus.

Family TRINUCLEIDAE Hawle and Corda 1847

Subfamily NOVASPINAE Whittington 1941

Genus NOVASPIS Whittington 1941

Novaspis aff. *albida* (Reed).

Plate 62, figs. 5–8

1862 *Trinucleus concentricus* Baily, p. 10.
1885 *Trinucleus concentricus* Baily, p. 29.
1939 *Trinucleus sp.* Harper (*in* Smyth and others), p. 303.
1942 *Trinucleus sp.* Harper, p. 276.

Material. Two cephala with portions of upper lamella of fringe, three cephala without fringe, five fragments of lower lamella, two fragments of upper lamella, five pygidia.

Description. Cephalon moderately convex, semicircular, twice as long as broad, posterior margin straight, produced into divergent genal spines. Glabella twice as long as broad, tapering posteriorly, expanded anteriorly into a strongly arched anterior lobe standing high above cheek lobes. Weak glabellar furrows form shallow pits behind anterior lobe. Cheeks as wide as long, posterolateral angles rounded. Posterior border upturned and extended laterally to support fringe; posterior border furrows broad and deeply impressed. Surface apparently smooth.

Fringe imperfect in all specimens; lower lamella produced into divergent genal spines of unknown length, bearing two E-rows of pits, the eight posterior pits in each row combining to form a single row of twin-pits. In upper lamella, fringe formula of I-rows I_1 1–19, I_2 1–19, I_3 18–19, I_4 19, with a pit in IRxix between I_3 and I_4. One anterior fragment of the outer part of the fringe probably belongs to the upper lamella; there are two rows of pits, in which the three anterior are combined as twin-pits.

Pygidium sub-triangular, $2\frac{1}{2}$ times as broad as long; axis gently convex, narrow, conical, the length of the pygidium, produced posteriorly into a short triangular tubercle; divided into seven rings, the first four distinctly defined. Pleural regions flattened, borders moderately convex and bent down vertically, wide laterally, narrowing to axial line. Three pairs of straight pleurae, two anterior distinctly defined, corresponding to two anterior axial rings; interpleural furrows moderately strongly impressed towards axis, becoming shallower outwards.

Remarks. In all features, including characters of the fringe, where determinable, the cephalon agrees with that of *Novaspis albida* (Reed) from the Upper Whitehouse Group, originally described as *Trinucleus* sp. ind. *b* (Reed 1904, p. 14, pl. 2, figs. 8, 8*a*), and subsequently assigned by the same author to the new species *T. albidus* (1914, p. 3, pl. 1, figs. 1, 2). Whittington (1941, p. 40) referred this species to *Novaspis*. The pygidium closely resembles that from Whitehouse described by Reed as *Trinucleus* sp. ind. *f*. (1904, p. 16, pl. 2, fig. 11).

Family DIONIDIDAE Gürich 1907, emend. Raymond 1920

Genus DIONIDE Barrande 1847

Dionide aff. *richardsoni* Reed

Plate 63, figs. 7, 8

Material. Three incomplete cephala, four pygidia.

Description. Cephalon gently convex, sub-semicircular in outline, $2\frac{1}{2}$ times as long as broad, posterior margin straight, anterior margin rounded. Glabella gently convex, out-

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EXPLANATION OF PLATE 62

The photographs are of natural internal moulds unless otherwise stated; they are untouched except for blacking-out of the matrix with process black. The specimens were lightly coated with ammonium chloride before being photographed.

Figs. 1–4. *Phylacops bituberculatus* sp. nov. 1, B.M. In. 53392. Holotype, cephalon; 1*a*, dorsal view ×10, showing large paired tubercles beside glabellar furrows; 1*b*, anterior view ×10, showing eyes separated by narrow band devoid of facets; 1*c*, lateral view ×10, showing right glabellar furrow and tubercle, and eye facets arranged in horizontal rows. 2, B.M. In. 53393, ×10. Paratype, pygidium, showing weakly segmented axis and faint interpleural furrows. 3, B.M. In. 53394, ×10. Late transitory pygidium with one segment in front of incompletely segmented posterior part. 4, B.M. In. 53395, ×10. Transitory pygidium with five fused segments.

Figs. 5–8. *Novaspis* aff. *albida* (Reed). 5, B.M. In. 53370. Small cephalon lacking most of fringe. 5*a*, Dorsal view ×10, showing fragments of inner part of upper lamella of fringe; 5*b*, lateral view ×10, showing arrangement of pits at posterolateral angle of fringe. 6, B.M. In. 53371, ×3. Fragment of posterior part of fringe of large individual; lower lamella, showing twinning of pits adjacent to girder. 7, B.M. In. 53372, ×10. Fragment of anterior part of fringe of small individual; external part of upper lamella, showing two rows of pits, the five anterior combined as twin-pits. 8, B.M. In. 53373, ×15. Small pygidium.

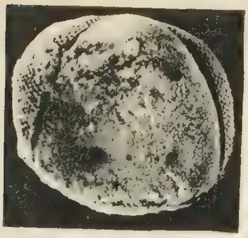
Figs. 9–10. *Dindymene ovalis* sp. nov. 9, B.M. In. 53388, ×7. Holotype, cephalon, showing rounding of genal angles, nearly straight axial furrows and posterior border furrows terminating adaxially in pits. 10, B.M. In. 53389, ×15. Paratype, pygidium, showing eight axial rings.

Figs. 11–15. *Thomondia globosa* Harper. 11, B.M. In. 53377, ×20. Incomplete cephalon, external mould, showing facial suture outside lateral border furrow. 12, B.M. In. 53380, ×25. Pygidium, external mould. 13, B.M. In. 53379, cranidium; 13*a*, lateral view ×20; 13*b*, dorsal view ×20. 14, B.M. In. 53378, ×20. Incomplete cephalon, external mould, showing right genal spine and posterior branch of facial suture. 15, B.M. In. 53376, ×15. Crushed dorsal shield with thorax impacted into pygidium.

Fig. 16. *Pseudosphaerexochus sp.* B.M. In. 53387, ×10. Incomplete cranidium.

Figs. 17–19. *Corrugatagnostus convergens* sp. nov. 17, B.M. In. 53368, ×10. Paratype, pygidium, showing almost square axis. 18, B.M. In. 53369, ×10. Paratype, cephalon, showing glabellar lobes produced forwards into discrete median ridges (posterior ridge damaged). 19, B.M. In. 53367, ×10. Holotype, cephalon, showing median furrow on preglabellar field reaching anterior border, and flanking furrows converging but not reaching border.

Fig. 20. *Remopleurides sp.* B.M. In. 53374, ×10. Cranidium.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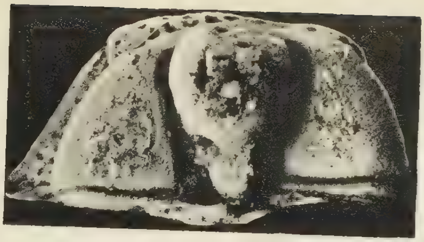
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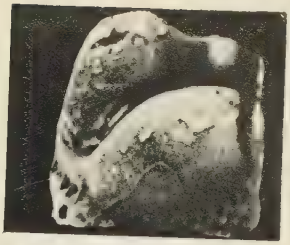
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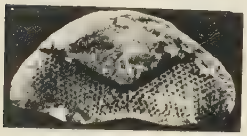
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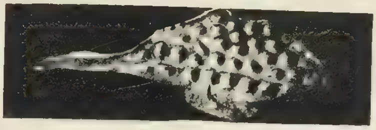
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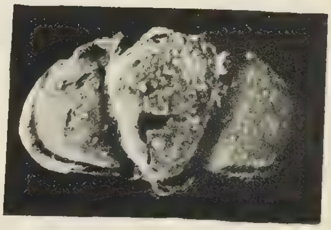
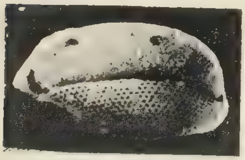

9 x 7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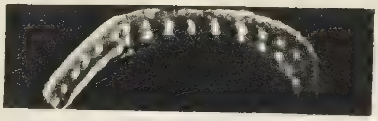
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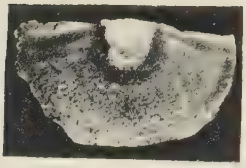
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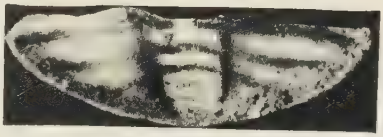
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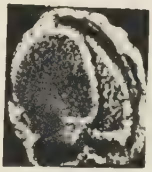
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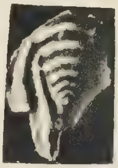
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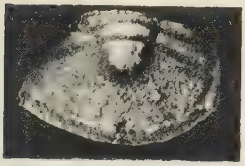
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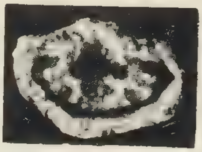
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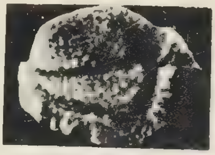
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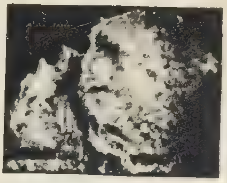
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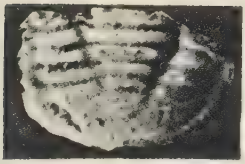
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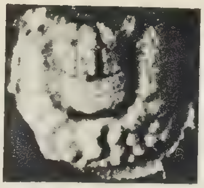
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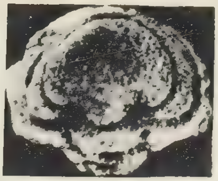
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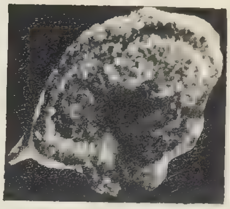
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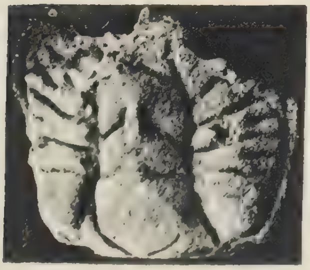
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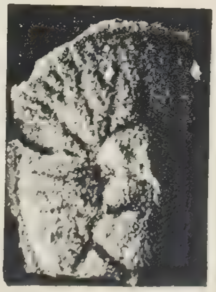
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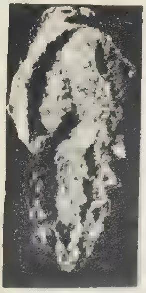
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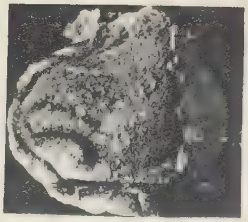

20 x 10

WEIR, Ashgillian trilobites

line subquadrate, smoothly rounded in front, three-quarters the cephalic length, axial and preglabellar furrows narrow. Cheeks gently convex, outline sub-triangular, margins steeply sloping. Genal caecae consisting of two ill-defined ridges commencing at half glabellar length, diverging and reuniting at posterolateral angle of cheek. Fringe moderately broad, continuing in front of glabella; cheeks and fringe bearing small pits in irregular arrangement. Posterior borders short (sag.), moderately convex, furrows broad and deeply impressed.

Pygidium semicircular in outline, slightly convex, length equal to breadth; axis gently convex, almost reaching posterior margin, conical, tapering from one-sixth the pygidial breadth anteriorly to a pointed termination, divided into twelve axial rings decreasing in sagittal length posteriorly, each bearing three circular muscle impressions, two lateral and one median. Pleural lobes flattened, margin bent downwards; twelve pairs of pleurae, widening gradually towards sides. Anterior pair directed outwards initially, bending downwards and slightly backwards beyond fulcrum; successive pleurae run more obliquely backwards with more acute bending beyond fulcrum. Interpleural furrows narrow and deeply impressed, not reaching margins. Inner parts of pleural regions bearing fine concentric ridges; outer parts smooth.

Remarks. In most observed characters the specimens agree with *Dionide richardsoni* Reed, first recorded (Reed 1904, p. 26, pl. 4, figs. 3–8) from the Drummuck Group (Upper Ashgillian) of the Girvan district, and subsequently by the same author from the Upper Whitehouse Group (1914, p. 5, pl. 1, fig. 3); but the glabellae of the Irish specimens are damaged and their features obscured. The fringe is more clearly demarcated from the cheeks than in the Girvan specimens; the pygidium agrees in all respects.

Family REMOPLEURIDIDAE Hawle and Corda 1847

Genus REMOPLEURIDES Portlock 1843

Remopleurides sp.

Plate 62, fig. 20

Material. One cranidium.

Description. Glabella moderately convex, sub-pentagonal, rounded in front, three-quarters as broad as long, anterior tongue one-fifth the glabellar length and one half its breadth, bent sharply downwards; two pairs of forwardly-diverging lateral glabellar furrows. Palpebral furrows weak, palpebral lobes narrow, linear. Occipital furrow deep, occipital ring long (sag.), becoming shorter laterally, strongly convex and moderately arched transversely. Surface apparently smooth.

Remarks. Some large eyes provisionally assigned to this genus by Baily (1862, p. 10) may belong to *Symphysops*; Baily's material is not available for study.

Family TELEPHINIDAE Marek 1952

Genus TELEPHINA Marek 1952

Telephina aff. *reedi* (Ulrich)

Plate 63, fig. 1

Material. Four cranida, one almost complete.

Description. Cranidium strongly convex, sub-pentagonal in outline, as long as broad; glabella extending to anterior border and two-thirds the cranidial breadth, strongly convex, tapering slightly forwards, anterior margin truncated and overhanging anterior border; posterior half bearing a faint ridge and numerous closely-set tubercles in irregular arrangement. Axial furrows broad and deeply impressed, becoming shallow forwards, preglabellar furrow broad but not deeply impressed; occipital furrow broad and shallow, almost dying out laterally, strongly arched forwards; occipital ring long (sag.) in axial line, strongly arched transversely and bearing base of median spine. Fixed cheeks crescentic in outline, strongly convex, breadth one-quarter the glabellar breadth. Palpebral lobes narrow, sickle shaped, extending the length of the fixed cheek, slightly concave behind and weakly convex in front; palpebral furrows broad and shallow, confluent anteriorly and posteriorly with axial furrows. Anterior border narrow, vertical, bearing a pair of short and slightly divergent spines directed vertically downwards.

Remarks. The anteriorly truncated glabella suggests relationship with *Telephina reedi* (Ulrich) from the Upper Whitehouse Group, the only species so far described with that feature (Ulrich 1930, p. 19, pl. 1, fig. 1; copy of Reed 1904, pl. 4, fig. 11); the species was first recorded by Reed (1904, p. 44) as *T. fractus* Barrande. The two cranidia here discussed differ from this and from other species in the strong convexity and relative narrowness of the glabella, but whether these differences are constant features of the Irish stock remains to be seen.

Family SHUMARDIIDAE Lake 1907

Genus SHUMARDIA Billings 1865

Shumardia extensa sp. nov.

Plate 63, figs. 5, 6

Holotype. B.M. In. 53383 (cephalon) Pl. 63, fig. 5. Dimensions: length of cephalon 1·3 mm., breadth of cephalon 2·5 mm., length of glabella 1·2 mm., breadth of glabella 1·2 mm.

Horizon and locality. Ballyvorgal Group (Ashgillian), Ballyvorgal South, Co. Clare, Ireland.

Diagnosis. Shumardia with isolated basal lateral glabellar lobes; glabella overhanging anterior margin. Posterior cephalic border furrows broad (sag.).

Description. Cephalon sub-semicircular in outline, moderately convex, half as broad as long; posterior margin slightly concave forwards, genal angles produced into short spines. Glabella sub-quadrate in outline, moderately convex, almost reaching anterior margin, as broad as long, rounded in front. Axial furrows broad and deeply impressed, preglabellar furrows less deeply impressed. Two pairs of lateral glabellar furrows; anterior pair short and straight, commencing at half the glabellar length and directed obliquely forwards to define a pair of lobate lateral expansions to anterior lobe, deeply impressed laterally and becoming weaker towards axial line, dying out at one-fifth glabellar breadth. Posterior part of glabella moderately convex, parallel-sided; posterior pair of lateral glabellar furrows deeply impressed adaxially, becoming less deep abaxially, commencing behind anterior pair and curving backwards to meet occipital furrow, defining small triangular basal lateral lobes. Occipital furrow broad, straight and deeply impressed from axial line to confluence with posterior lateral glabellar furrows, bending backwards behind basal lateral lobes. Occipital ring of moderate and uniform sagittal length, moderately arched transversely, gently convex longitudinally.

Cheeks sub-triangular in outline, narrowing anteriorly, strongly convex, bending vertically downwards, continuing anteriorly in narrow vertical preglabellar field, produced posteriorly into short backwardly-directed genal spines. Posterior borders moderately long (sag.), posterior border furrows broad, deeply impressed, directed obliquely backwards.

Remarks. The holotype differs from the syntype of *Shumardia scotica* Reed (1904, p. 42, pl. 4, fig. 12; B.M. In. 21165) from the Upper Whitehouse Beds in the anterior rounding of the glabella and in its greater anterior extension; other specimens of *S. scotica* in the Gray Collection have a glabella more extended than the syntype mentioned, but never so extended as to overhang the anterior margin.

One immature cephalon (Pl. 63, fig. 6) is ascribed to the new species; the glabella is relatively shorter, the preglabellar field wide and the occipital ring bears a tubercle. In the holotype the occipital ring is incomplete and the tubercle probably broken away.

Family ISOCOLIDAE Angelin 1854

Genus THOMONDIA Harper 1942

The discovery of additional material from the type locality (Harper 1942) enables a new and expanded account to be given; Harper described the cranidium only.

Diagnosis. Isocolidae with a single pair of pit-like lateral glabellar furrows confluent with occipital furrow; lateral border furrows confluent with preglabellar furrow; facial sutures situated on lateral border.

Thomondia globosa Harper

Plate 62, figs. 11–15

1942 *Thomondia globosa* Harper, pp. 276–8, pl. 4, figs. 1–8.

Material. One complete dorsal shield, three cephala, seventy cranidia, four pygidia, two detached thoracic segments.

Diagnosis. As for the genus.

Description. Body elongate, sub-ovate, twice as long as broad. Cephalon and thorax of about equal length, pygidium one-sixth length of body.

Cephalon strongly convex, parabolic in outline, length equal to breadth; surrounded anteriorly and laterally by narrow, steeply inclined border produced into short, broad, projecting genal spines.

Glabella four-fifths the cephalic length, defined by strongly-impressed axial and preglabellar furrows, strongly convex, arched downwards. One pair of lateral glabellar furrows, broad and deeply impressed, length one-third glabellar breadth, deepening into prominent pits on either side of glabella behind large anterior lobe and confluent with occipital furrow. Occipital ring long (sag.) in axial line, narrowing to points laterally, moderately convex longitudinally, strongly arched transversely, bearing a median tubercle. Occipital furrow deeply impressed, broad and straight.

Fixed cheeks sub-triangular, bent downwards, slightly convex. Posterior border narrow, raised and rounded; posterior border furrows broad and deeply impressed. Lateral borders of uniform width posteriorly, anterior borders widening slightly to axial line. Strong lateral border furrows coalesce anteriorly with preglabellar furrow and posteriorly with posterior border furrows. Anterior branches of facial sutures converge strongly, posterior branches run parallel to lateral border furrow to cut posterior border. Eyes not preserved. Free cheeks narrow, elongate, produced posteriorly into a pair of short divergent genial spines.

Thorax composed of not more than six segments, moderately convex, narrowing slightly posteriorly. Axis strongly convex, one-third breadth of thorax. Pleurae straight, horizontally extended to fulcrum, outer parts steeply inclined. Pleural furrows broad and deep, parallel to articulating furrows; pleural bands reduced to narrow ridges.

Pygidium small, semi-oval, twice as broad as long. Axis convex, four-fifths the pygidial length and one-third its breadth, tapering to a rounded extremity; consisting of two narrow, rounded axial rings and a short terminal piece. Ring furrows broad and shallow, terminating laterally in shallow pits; axial furrows broad and deep. Pleural regions taper posteriorly and continue round posterior extremity of axis; divided into three pairs of strongly convex pleurae. Interpleural furrows broad and deeply impressed, not reaching pleural margins. Border depressed. *Dimensions of complete dorsal shield* (B.M. In. 53376, Pl. 62, fig. 15): length (estimated) 2·4 mm. (cephalon impacted into thorax; estimated total length 3·0 mm.), length of cephalon 1·3 mm., length of thorax 1·3 mm., length of pygidium 0·4 mm.

Remarks. Thomondia agrees with Whittington's emended diagnosis of the Family Isocolidae (1956, p. 1194) in all characters except the posterior position of maximum glabellar breadth. It is proposed accordingly that *Thomondia* should be placed in the

EXPLANATION OF PLATE 63

The photographs are of natural internal moulds unless otherwise stated; they are untouched except for blacking-out of the matrix with process black. The specimens were lightly coated with ammonium chloride before being photographed.

Fig. 1. *Telephina* aff. *reedi* (Ulrich). B.M. In. 53375, cranidium; 1*a*, lateral view ×7; 1*b*, anterior view ×7, showing anterior spines bent down vertically and high convexity of glabella; 1*c*, dorsal view ×7, showing truncated anterior margin of glabella.

Figs. 2, 3. *Staurocephalus* aff. *murchisoni* Barrande. 2, B.M. In. 53385, ×7. Detached glabella. 3, B.M. In. 53386, ×15. Pygidium.

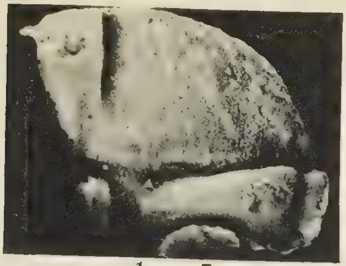
Fig. 4. Cyclopygid pygidium. B.M. In. 53396. 4*a*, Dorsal view ×7, showing indistinctly defined axis with five pairs of muscle impressions; 4*b*, lateral view ×7.

Figs. 5, 6. *Shumardia extensa* sp. nov. 5, B.M. In. 53383, holotype, cephalon; 5*a*, lateral view ×15, showing glabella overhanging vertical preglabellar field; 5*b*, anterior view ×15; 5*c*, dorsal view ×15, showing two pairs of lateral glabellar furrows, posterior pair indistinctly defined. 6, B.M. In. 53384, ×25. Young cephalon, external mould, showing relatively small glabella, wide preglabellar field and tubercle on occipital ring.

Figs. 7, 8. *Dionide* aff. *richardsoni* Reed. 7, B.M. In. 53382, ×10. Pygidium. 8, B.M. In. 53381, ×15. Incomplete cephalon showing faintly defined genal caecae.

Fig. 9. *Trinodus? sp.* B.M. In. 53366, incomplete cephalon; 9*a*, dorsal view ×12; 9*b*, lateral view ×12.

Figs. 10, 11. *Symphysops* aff. *subarmatus* (Reed). 10, B.M. In. 53391, ×5. Pygidium. 11, B.M. In. 53390, ×3. Free cheek with portion of eye.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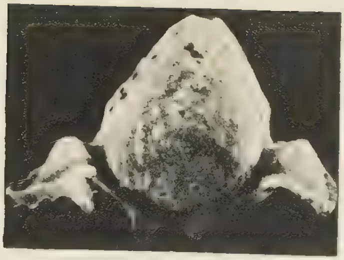
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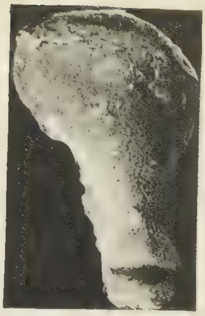
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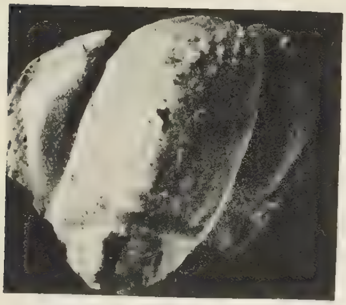
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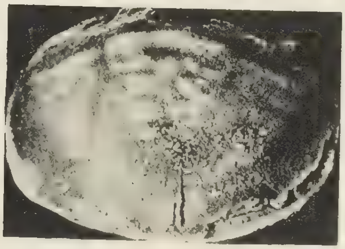
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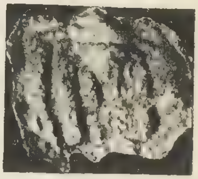
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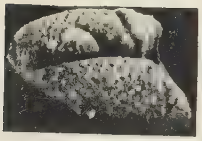
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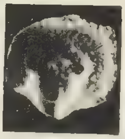
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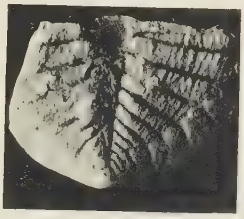
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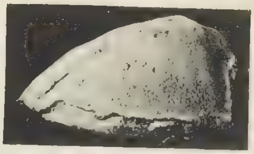
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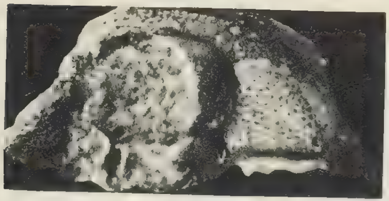
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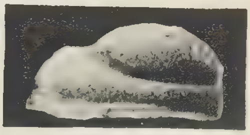
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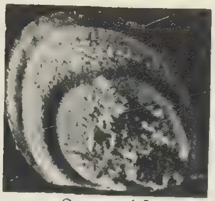
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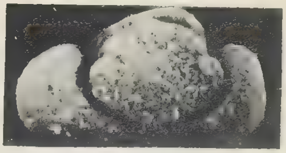
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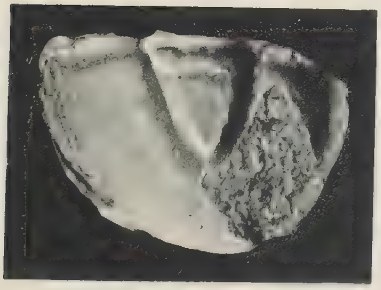
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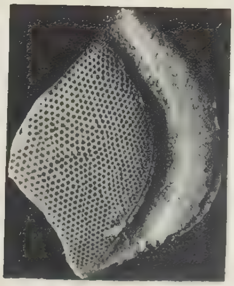
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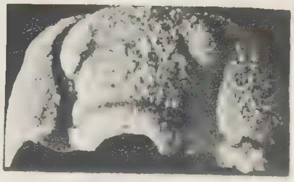
5c x 15

WEIR, Ashgillian trilobites

Isocolidae, this assignment requiring that the words 'greatest width at, or in front of, mid-length' in Whittington's family diagnosis be deleted.

In most of its features *Thomondia* compares closely with *Cyphoniscus* from the Chair of Kildare Limestone (Whittington 1956, p. 1195, pl. 130, figs. 1–9, 11, 12; text-figs. 2*a*, *b*), especially in the characters of the glabella and in the confluence of the posterior and lateral border furrows. The glabella is intermediate between that of *Isocolus* from the Kallholn Limestone of Dalarne, Sweden (Whittington 1956, p. 1194, pl. 129, figs. 1–11; text-figs. 1*a*, *b*), which has two pairs of lateral glabellar furrows, and *Cyphoniscus*, with none; the glabella of *Thomondia* could be derived from one of the *Isocolus* type by suppression of the anterior glabellar furrows and enlargement of the posterior furrows till they coalesce with the occipital furrow and obliterate the outer parts of the posterior glabellar lobe. *Thomondia* differs from other Isocolids in the anterior coalescence of the lateral border and preglabellar furrows and in the situation of the facial suture on the lateral border.

Family CYCLOPYGIDAE Raymond 1925

Genus PHYLACOPS Cooper and Kindle 1936

Phylacops bituberculatus sp. nov.

Plate 62, figs. 1–4

1862 *Aeglina rediviva* Baily, p. 10.
1885 *Aeglina rediviva* Baily, p. 29.
1939 *Cyclopyge rediviva* Stubblefield, p. 61.
1939 *Cyclopyge* cf. *rediviva* Harper (*in* Smyth and others), p. 303.
1942 *Cyclopyge* spp. nov. Harper, p. 276.
1948 *Cyclopyge* Harper, p. 60.

Material. Holotype: B.M. In. 53392 (cephalon), Pl. 62, fig. 1. Dimensions of holotype: length of cephalon 2·8 mm., breadth of cephalon 3·0 mm., breadth of glabella 2·5 mm. Paratype: B.M. In. 53393 (pygidium), Pl. 62, fig. 2. Dimensions of paratype: length of pygidium 1·7 mm., breadth of pygidium 3·4 mm., length of axis 0·7 mm. Other material: 49 cranidia, 3 pairs of connected free cheeks, 10 detached eyes, 98 pygidia.

Horizon and locality. Ballyvorgal Group (Ashgillian), Ballyvorgal South, Co. Clare, Ireland.

Diagnosis. Phylacops with oblique lateral glabellar furrows placed far back; one pair of tubercles situated between lateral glabellar and occipital furrows.

Description, Body oval in outline, convexity moderate anteriorly, decreasing posteriorly. Cephalon subcircular, moderately convex. Glabella sub-triangular, slightly longer than wide, anterior margin abruptly, posterior gently rounded. Lateral glabellar furrows oblique, discontinuous anteriorly and posteriorly and placed far back; a pair of large, ill-defined tubercles situated between lateral glabellar and occipital furrows. Median tubercle absent. Axial and preglabellar furrows coincident with palpebral furrows, faintly defined. Occipital ring broad and short (sag.), slightly convex forwards, moderately arched transversely, narrowing to points laterally; occipital furrow narrow. Palpebral lobes narrow, concave, continuing round front of glabella and extending backwards to occipital furrow. Facial sutures run parallel to axial and preglabellar furrows, joining anteriorly. Free cheeks uniting in front of glabella, forming narrow vertical band separating eyes. Eyes large, elongate, length three times the breadth and equal to the glabellar length, extending to lateral border and anteriorly to doublure; facets hexagonal, arranged in fourteen alternating horizontal rows of thirty-five facets each; total number of facets approximately 490. Lateral borders narrow, concave, almost vertical; lateral border furrows indistinct, becoming obsolete at one-fifth cephalic length, in front of which border turns under to merge with doublure, which widens thence to axial line. Doublure with closely-set striations parallel to outer margins of eyes.

Thorax of unknown number of segments presumably of uniform breadth, moderately convex; axis narrow posteriorly, widening rapidly anteriorly, gently convex; axial furrows moderately deeply impressed and broad. Axial rings short, of equal length, posterior part convex, anterior part concave; articulating furrows narrow. Pleurae gently convex, anterior pleural bands narrow, posterior wider; pleural furrows broad and shallow.

Pygidium transversely semi-oval, twice as broad as long, moderately convex, anterior margin gently rounded; axis semi-oval, length equal to anterior breadth and two-fifths pygidial length, convex, divided into three weakly-defined axial rings; articulating half-ring short (sag.) and strongly convex. Pleural regions divided into three pleurae of unequal size by two pairs of poorly-defined interpleural grooves corresponding in position to axial ring furrows, the two anterior pleurae together occupying one-fifth the pygidial length; anterior pleurae with narrow pleural bands, pleural furrows broad and shallow. Border moderately convex, broadening postero-laterally and narrowing to axial line; doublure coincides in extent, inner surface bearing faint concrescent striations. Border furrows moderately impressed.

Remarks. No complete specimen was found; the characters of the thorax, as far as determinable, were deduced from numerous transitory pygidia with up to five fused segments in front of the large posterior segment.

P. bituberculatus closely resembles *P. kloučeki* (Richter) from the Svata Dobrotiva Shales (Dγ_2, Llandeilo) of Malé Přilepy, Bohemia (Whittard 1952, p. 310, pl. 32, fig. 9), in the separation of the eyes by a narrow band devoid of facets, but is considerably smaller; from the figure, the eye facets in *P. kloučeki* appear to be much more numerous and closely packed. The other Irish species, *P. mirabilis* Forbes MS., Salter from the Portraine Limestone (Whittard 1952, p. 309, pl. 32, figs. 6–8), lacks the distinct band separating the eyes, has the facets arranged in vertical rows, and possesses a single median tubercle.

Genus SYMPHYSOPS Raymond 1925

Symphysops aff. *subarmatus* (Reed)

Plate 63, figs. 10, 11

Material. Four free cheeks, one pygidium.

Description. Pygidium semi-oval, moderately convex, length equal to breadth, anterior margin gently rounded; axis triangular with a short triangular terminal piece, moderately convex, one half the pygidial length, with a single, weakly-defined axial ring at one-fifth the axial length; axial furrows broad and deeply impressed. Pleural regions moderately convex, bearing five pairs of poorly-defined interpleural grooves. Borders narrow, convex, and smooth; border furrows deeply impressed.

Remarks. This pygidium corresponds in most respects to that of *Symphysops subarmatus* (Reed) (1914, pl. 3, fig. 9), except in relative breadth, which is much greater in Reed's figured specimen. Four detached free cheeks with portions of the eye compare with that figured by Reed (1904, pl. 7, fig. 14) and assigned by him firstly to *Cyclopyge armata* (Barrande) and later (1914, p. 21) to the new species *C. subarmata.*

Cyclopygid gen. et sp. indet.

Plate 63, fig. 4

Material. One pygidium.

Description. Transversely semi-oval, moderately convex, two-thirds as long as broad, anterior margin gently rounded. Axis poorly defined, half the pygidial length, triangular in outline, apex rounded; consisting of five weakly-defined rings, each ring bearing a pair of circular muscle impressions laterally. Pleural regions moderately convex, triangular in outline. Border concave, depressed, broadening posteriorly to half the pygidial length, narrowing thereafter towards median line and becoming weaker. Inner surface of doublure ornamented by fine, irregular, concentric furrows.

Remarks. This pygidium resembles that of *Cyclopyge bumasti* Reed (1914, p. 19, pl. 3, fig. 8) in the weakly-defined axis with poor segmentation.

Family CHEIRURIDAE Hawle and Corda 1847

Genus PSEUDOSPHAEREXOCHUS Schmidt 1881

Pseudosphaerexochus sp.

Plate 62, fig. 16

Material. One cranidium.

Description. Cranidium triangular in outline, rounded in front, moderately convex, $2\frac{1}{2}$ times as long as broad. Glabella subcircular, truncated behind, reaching front of cranidium, tumid, defined by deeply-impressed axial furrows. Lateral glabellar furrows broad and shallow, anterior pair one-third breadth of glabella, commencing at anterior extremity of fixed cheek and directed obliquely backwards; middle pair one-quarter the glabellar breadth, transversely directed; posterior pair oblique, confluent with occipital furrow and enclosing a small pair of triangular basal lateral lobes. Occipital furrow broad and deeply impressed, occipital ring strongly arched transversely. Cheeks triangular in outline, three-quarters the cephalic length, posterior border furrow deeply impressed.

Genus STAUROCEPHALUS Barrande 1846

Staurocephalus aff. *murchisoni* Barrande

Plate 63, figs. 2, 3

1862 *Staurocephalus globiceps* Baily, p. 10.

Material. Two cranidia, three pygidia.

Description. Glabella anteriorly inflated, $1\frac{1}{2}$ times as long as broad; divided into two parts by anterior glabellar furrows. Anterior lobe tumid; posterior lobe short, tapering slightly forwards, strongly convex. Anterior lateral glabellar furrows continuous, straight and weak; middle and posterior pairs reduced to small lateral pits equally spaced. Occipital furrow strong and straight, occipital ring short and convex, moderately arched transversely, slightly concave forwards. Cheeks not preserved.

Pygidium subquadrate, flattened; axis strongly convex, sharply conical, half the pygidial length; anterior part tapering rapidly posteriorly, carrying three rings short and convex lengthwise, ring furrows broad and deep; posterior part unsegmented and tapering less rapidly. Pleural regions consisting of three pairs of flattened pleurae in close contact throughout their length and of uniform breadth, corresponding to rings on anterior part of axis; inner part of anterior pair transverse, turning sharply backwards at one-third the length to lie parallel to axis, bearing short pleural furrows adaxially; second and third pairs turn backwards progressively closed to axis and lack pleural furrows. A flattened plate is assumed to correspond to a fused pair of pleurae, their pointed extremities forming short projections from hinder margin.

Remarks. The strongly inflated anterior glabellar lobe is characteristic of *Staurocephalus*; the typically cheirurid pygidium is distinctive of *S. murchisoni* Barrande (Reed 1898, p. 213) and generally similar to those figured by Barrande (1852, pl. 43, figs. 28, 31).

Family ENCRINURIDAE Angelin 1854

Genus DINDYMENE Hawle and Corda 1847

Dindymene ovalis sp. nov.

Plate 62, figs. 9, 10

1862 *Dindymene haidingeri* Baily, p. 10.
1885 *Dindymene haidingeri* Baily, p. 29.
1939 *Dindymene* Stubblefield, p. 61.
1942 *Dindymene haidingeri* Harper, p. 276.
1948 *Dindymene* Harper, p. 60.

Material. Holotype: B.M. In. 53388 (cephalon), Pl. 62, fig. 9. Paratype: B.M. In. 53389 (pygidium) Pl. 62, fig. 10. Other material: seven cephala, one pygidium.

Horizon and locality. Ballyvorgal Group (Ashgillian), Ballyvorgal South, Co. Clare, Ireland.

Diagnosis. Dindymene with cephalon bearing sparse small tubercles, axial furrows slightly convex outwards, genal angles smoothly rounded and cheek lobes sub-semicircular in outline.

Description. Cephalon nearly oval in outline, twice as broad as long, moderately convex. Glabella pyriform, strongly convex, extending in front of cheek lobes, length slightly greater than breadth, narrowing posteriorly to less than half the breadth, bearing a large median tubercle near posterior extremity; lateral glabellar furrows absent. Axial furrows broad, deeply impressed, almost straight but slightly convex outwards. Occipital ring short (sag.) and narrow, strongly arched longitudinally and transversely, occipital furrow broad and shallow. Cheek lobes much less highly elevated than glabella, sub-semicircular in outline; genal angles smoothly rounded. Lateral borders of moderate breadth, narrowing anteriorly, gently convex, sloping slightly downwards, lateral border furrows deeply impressed posteriorly, becoming shallower forwards. Posterior border continuous laterally with lateral border, narrowing and turning backwards towards axial line, gently convex. Posterior border furrows strongly impressed, joining axial furrows in shallow pits. Facial sutures, eyes and palpebral lobes absent. Thorax unknown.

Pygidium narrow, length slightly less than breadth; axis half pygidial length, conical, apex pointed, composed of seven rings. Axial rings short and strongly convex (sag.), of equal length; moderately arched transversely. Ring furrows deeply impressed, continuous. Axial furrows narrow and weak. Pleural regions composed of two pairs of pleurae, corresponding to two anterior axial rings; strongly curved backwards to lie parallel to axis, free for half their length beyond posterior extremity of axis, points slightly curved outwards.

Remarks. The shape of the glabella is similar to that of *D. cordai* Nicholson and Etheridge (Reed 1906, p. 132, pl. 17, fig. 9) from the Drummuck Group (Ashgillian) of the Girvan district, though this species differs in the greater acuteness of the genal angle and the relatively longer pygidial axis; the pygidium of *D. ovalis* resembles that of *D. haidingeri* Barrande (1852, p. 819, pl. 43, fig. 25) in most respects, but the cephalon is very different, *D. haidingeri* having well-developed genal spines and a relatively broader glabella with the axial furrows concave outwards. *D. ovalis* also differs from the above species in the poorly-developed tuberculation.

Family BOHEMILLIDAE Barrande, 1872

Genus BOHEMILLA Barrande, 1872

Bohemilla sp.

1862 *Olenus?* Baily, p. 10, text-fig. 1*b*.
1939 *Bohemilla* Stubblefield, p. 61.
1939 *Bohemilla* Harper (*in* Smyth and others), p. 303.
1942 *Bohemilla* Harper, p. 276.
1948 *Bohemilla* Harper, p. 60.
1952 *Bohemilla* Whittard, p. 319.

The specimen in the collection of the Geological Survey of Ireland, figured by Baily and subsequently determined from the figure as *Bohemilla* by Stubblefield, is unfortunately not available for study; no other specimen was found.

COMPARISON WITH OTHER *CYCLOPYGE* FAUNAS

The mudstone band yields a prolific shelly fauna without graptolites, in which trilobites greatly outnumber all other forms both in species and in individuals; all are disarticulated except one dorsal shield of *Thomondia*. Of particular interest is the assignment of this genus to the Family Isocolidae, this being the first definite record of an isocolid from other than a reef-limestone facies. The most abundant member of the fauna is *Phylacops bituberculatus* sp. nov., ninety-eight pygidia in various stages of development and fifty cranidia having been collected. *Thomondia* comes second in order of abundance with seventy cranidia.

As Baily (1862, p. 10) and Stubblefield (1939, p. 61) have shown, the Slieve Bernagh tribolite bed contains several species closely related to forms occurring in Bohemia, mostly in the Kv̌án Series ($D\gamma_1$, Llanvirn-Llandeilo), though certain genera are found also in the *D. bifidus* zone in Wales. The following species appear to be of Bohemian derivation:

	Number o specimens
Corrugatagnostus convergens sp. nov.	9
Dionide richardsoni Reed	7
Phylacops bituberculatus sp. nov.	160
Symphysops aff. *subarmatus* Reed	5
Cyclopygid gen. et sp. indet.	1
Staurocephalus aff. *murchisoni* Barrande	5
Dindymene ovalis sp. nov.	10
Total	197

Other species total 105 specimens, the percentage of forms of Bohemian affinity being sixty-five, a remarkably large proportion considering the difference in geological age between the faunas.

The fauna with which the closest comparison can be made is that of the Upper Whitehouse Beds of the Girvan District, Ayrshire, which was clearly derived from the main Bohemian source, though the species are more specialized. Twelve of the fifteen Slieve Bernagh genera (all except *Thomondia*, *Pseudosphaerexochus* and *Staurocephalus*) and the four species *Novaspis albida* (Reed), *Dionide richardsoni* Reed, *Telephina reedi* (Ulrich), and *Symphysops subarmatus* (Reed) occur in the Whitehouse Beds, both horizons being considered to belong to the zone of *D. complanatus*.

Cyclopyge faunas appear at various other horizons in the Upper Ordovician of the British Isles and Ireland, for instance in the Abercwmeiddaw Group of the area around Corris, Dinas Mawddwy, and Towyn, above the *Phillipsinella parabola* Beds (Pugh 1923, 1928), and in the Oriel Brook Mudstone of Grangegeeth, Co. Meath, which may be of *Pleurograptus linearis* age (Harper 1952). The occurrence of *Phylacops mirabilis* Forbes MS., Salter and *Staurocephalus* at Portraine (Gardiner, Reynolds, and Reed 1897) and of *Cyclopyge rediviva* Barrande in the Upper Tirnaskea Beds of Pomeroy, Co. Tyrone (Fearnsides, Elles, and Smith 1907), in association with *D. mucronatus* indicates the firm establishment of those genera of Bohemian origin in the Irish faunas, whereas few of the exotic Whitehouse forms survived in the Girvan area till Drummuck times. Stubblefield (1939, p. 62) postulated an Upper Ordovician migration from Central Europe to Scotland, possibly through Co. Clare and Co. Tyrone, with a diversion to Central Wales.

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GONIATITES STRIATUS AND RELATED FORMS FROM THE VISÉAN OF IRELAND

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ABSTRACT. Five goniatite species, of which two are new, are described from the P_{1b} subzone of the Upper Viséan shales of Dough Mountain, Co. Leitrim, Ireland. These species are diagnosed mainly on the test ornamentation which is claimed to be continuously variable and is arbitrarily divided into stages. Goniatites, the mature ornament of which belongs to a particular stage, are named as separate morphological species. The succession of ornament stages constitutes a trend which has operated upon a primitive stock both in B_2 and P_{1b} times. This has led to the production of homeomorphs the separation of which is important in stratigraphical studies.

INTRODUCTION

IN the P_{1b} subzone of the Bollandian occurs a closely related group of goniatites including the subzonal index fossil *Goniatites falcatus* Roemer and also *G. striatus* (J. Sowerby). Collecting from the Leitrim Shales in the Dough Mountain area, between Manorhamilton and Kiltyclogher, Co. Leitrim, Ireland, has provided an abundant suite of well-preserved goniatites from this subzone, which is about 50 feet thick. Scattered goniatites are to be found throughout this thickness, but by far the most prolific horizon occurs about 6 feet above a thin sandstone at the base. When making the collection, specimens from different stratigraphical levels were not separately labelled but it can be definitely stated that examples of all the species described in this paper occur in this thin prolific bed.

It may be that if all levels provided such an abundance of specimens that the numerical proportions of the different species would vary in a systematic manner according to the stratigraphic level. Since, however, only single specimens are known from most levels, we have not sufficient data to establish this. Kobold (1933, p. 471) collecting from successive thin beds within this subzone in Germany claimed a stratigraphical succession of species of this group of goniatites which we have not been able to corroborate.

Registration numbers preceded by the letters G.S.M. or B.M. are, respectively, those of specimens in the Geological Survey Museum, London, and the British Museum (Natural History).

SHELL ORNAMENTATION

In the *Goniatites striatus* group the succession of shell ornament stages, when complete, is as follows:

1. In individual development the earliest type consists of roughened to crenulate transversals only. In the young these are forwardly bowed over the venter. This is the *crenistria*-stage.

2. Increase in the crenulation of the transversals gives rise to spirals which increase in strength until they equal the transversals. This reticulate pattern is the *concentricus*-stage.

3. Then the transversals weaken whilst the spirals retain their strength so that they become the dominant feature of the ornament over the entire shell. This domination may be achieved at different diameters on different regions of the shell, i.e. near the

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umbilical border, on the flanks, and over the venter. When the spirals are dominant this is called the *striatus*-stage.

4. Then follows a stage in which transverse elements reappear. This is a result of periodic appearance of thin grooves, fairly distantly spaced, dividing the surface of the shell into 'straps' upon which up to twelve faint transverse growth-lines may be accommodated. This is the *spirifer*-stage.

5. The grooves deepen and widen and the 'straps' become ribs of the 'dip escarpment' type with the steep slope facing forwards. This is the *radiatus*-stage.

6. The development of a bow, convex forward, near to the umbilical edge leads to the final *falcatus*-stage.

Each of the stages 2 to 6 may constitute the adult ornament of a particular form of the *striatus* group and in such cases the form is here named as a species.

DESCRIPTIONS OF SPECIES

Goniatites concentricus sp. nov.

Plate 64, figs. 1–3, 5–8; Plate 65, fig. 6

Glyphioceras intermedium Kobold MS., Haubold 1930, p. 78.
Glyphioceras intermedium Kobold 1933, p. 487, pl. 22, figs. 2–4.
Goniatites cf. *intermedium* Moore 1936, p. 187, pl. 3, fig. 3.
Non *Goniatites intermedium* Brown 1841, p. 215; 1849, p. 248.

Holotype. G.S.M. 87221 (Pl. 64, fig. 7), Dough Mountain, Co. Leitrim, Ireland.

Horizon. Viséan, P_{1b} subzone of the English goniatite zonal scheme; subzone IIIα/β to IIIβ_2 of the German scheme (*fide* Kobold 1933).

Discussion of the name. The name *Goniatites intermedius* Kobold could be used for this species if it were not preoccupied by *G. intermedium* Brown. Since Kobold's original material was indifferently preserved we have preferred to erect a new species based on well-preserved Irish material rather than simply to rename Kobold's species.

Dimensions (in mm.)

Diameter	*Thickness*	*T/D%*	*Umbilicus plus inner area*	*U/D%*
28·7	18·2	63	5·5	19·0
33·5	21·0	63	6·0	18
36·1	26·0	72	6·0	17
42·3	25·1	60	6·5	15·5
28·2	20·6	73	6·5	23
49·0	28·3	58	7·0	14
26·6	18·8	70	. .	. .

Description. In his description of *Glyphioceras intermedium*, Kobold emphasized the intermediate character of his species, especially as regards the ornament, between *G. crenistria* on the one hand and *G. striatus* on the other. In the former the ornament consisted of crenulate transversals only whereas in the latter spirals were the dominant element of the shell ornament. The stratigraphical position claimed by Kobold for his species on the basis of his own collecting was not inconsistent with his hypothesis.

A specimen (G.S.M. 87225), presumed to be the young of this species, is shown on Pl. 64, figs. 1 and 2. At 10 mm. shell diameter the thickness is 85 per cent. The ornament consists dominantly of crenulate transversals spaced at 4½ per mm. on the centre of the venter. These leave the umbilicus with a forward direction and describe a shallow, forwardly directed bow on the lower parts of the flanks from which they bend backward to make a slight sinus in the middle of the flanks. From this they pass into a very slight lingual bow at the site of the future latero-ventral shoulder. Over the venter, even at this diameter, a faint hyponomic sinus may be seen (Pl. 64, fig. 2). One faint constriction is visible through the test. Faint spirals are present. Pl. 64, fig. 1 shows these appearing around the umbilical edge about half a whorl behind the aperture. They can be seen to result from the strengthening and alignment of the 'teeth' of the crenulations on the transverse striae. Faint, incipient distant spirals can be detected on the site of the latero-venter.

The holotype shows the mature test ornament. The same elements of the transversals already recognized in the above-described nucleus are recognizable, but the sinus in the middle of the flanks is almost obliterated and the transversals are straight in this region. Moreover, the lingual bow has not developed and is a minor feature of the swinging course of the transversals. On the other hand, the hyponomic sinus is now an appreciable feature. Spirals are distributed all over the shell but remain stronger around the umbilicus and on the latero-venter and the venter.

The suture line (text-fig. 1) shows a high median saddle and a ventral lobe with divergent sides. The first lateral lobe has an asymmetric, narrowly rounded top. The lateral lobe is not as narrow as that of *G. falcatus* but less wide than that of *G. striatus* and is slightly deeper than the ventral lobe and with slightly accuminate tip.

Internal characters. A specimen sectioned at right angles to the plane of bilateral symmetry passed slightly in front of the protoconch so that the nucleus of Pl. 64, fig. 6 is the first whorl. Although not quite median, the section was measured at half-whorl intervals since the errors in dimensions of such a section would be very small in the outer whorls. Since the section is figured it is not necessary to do more than mention the salient features. The ratio of thickness to shell diameter shows that the shell is almost spherical until the end of the fifth whorl. After that the whorl height increases slowly at first and, at the commencement of the sixth whorl, much more rapidly, so that the ratio decreases from 92 per cent. at the fifth whorl to 61·5 per cent. at 8½ whorls when the diameter is 38·8 mm.

The umbilicus is about 16 per cent. of the diameter between the fifth and seventh whorls, but although the absolute size continues to increase, the ratio of umbilicus to diameter decreases slowly to 13·5 per cent. at 38·8 mm. diameter. The umbilical edge is sharply rounded and there is no inner area, the umbilical slopes being undercut. The greatest width is near the umbilical edge at the line of involution.

A section nearly along the plane of symmetry of a completely septate specimen shows 8¾ whorls (Pl. 64, fig. 5). There are 7 septa in the first and 6 in the second whorl. At 2½ whorls the density of septation increases so that there are 13 septa in the third and 15 in the fourth whorls. In the next four whorls the septa number between 15 and 17 per whorl and there are 17 in the last three-quarters of a whorl, which probably indicates the usual more closely-spaced septa which occur immediately behind the body chamber. At the greatest diameter seen, the siphuncle is about 0·5 mm. in diameter. The siphuncle increases in diameter very slowly, so that although it occupies about 17 per cent. of the whorl height in the fifth and sixth whorls, it occupies only about 9 per cent. in the seventh and eighth whorls. The septal necks are retrosiphonate to the maximum diameter seen. This is usual in Lower Carboniferous goniatites. Details of the very early behaviour of the siphuncle are unfortunately not seen in this section.

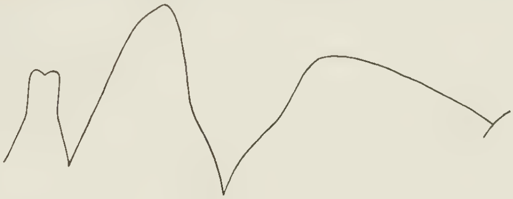


FIG. 1

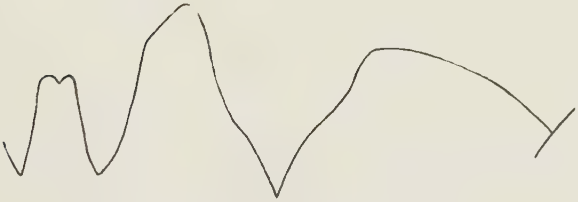


FIG. 2

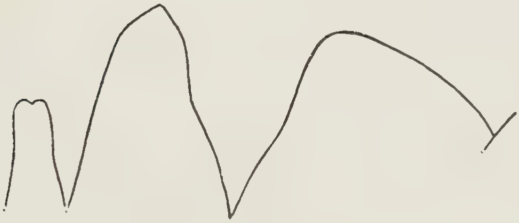


FIG. 3

TEXT-FIGS. 1–3. Suture lines magnified 100/diameter in mm. 1, *Goniatites concentricus* sp. nov., G.S.M. Zl 7315 at 26 mm. diameter, ×3·85. 2, *G. falcatus* Roemer, G.S.M. Zl 3762 at 30 mm. diameter, ×3·33. 3, *G. falcatus*, G.S.M. Zl 4033 at 46 mm. diameter, ×2·18.

Variation. Specimen G.S.M. 87224 (Pl. 64, fig. 3) is a variety with much finer transversals than the type. Specimens are known in which the spirals are absent and in this respect resemble the presumed ancestral *G. crenistria* but differ in the more sinuous course of the transversals and particularly in the deeper hyponomic sinus. They are also thinner than typical *G. crenistria* at the same diameter. Variants also occur in which the spirals are present around the umbilicus but lacking at the latero-venter. Such is typified by G.S.M. 87222 figured in Pl. 64, fig. 8. On the other hand, variants are seen in which the spirals are stronger and more evenly distributed than in the type. A typical example of this variant is shown on Pl. 64, fig. 4. This might be regarded as transitional to *G. striatus* but is also strongly resembled by the specimen G.S.M. 85641 figured by Bisat (1952, pl. 1, fig. 4) from 10 feet below the *G. falcatus* band at Cowdale Clough, Barnoldswick, Yorks., and referred to '*G. crenistria* late form'. Our variant differs in the more sinuous course of the transversals and in the presence of an appreciable hyponomic sinus and in the smaller umbilicus. Nevertheless, the resemblance is close enough to warrant the supposition that the Irish and Yorkshire beds which yielded these specimens are nearly on the same stratigraphical horizon. Specimen G.S.M. 87223 (Pl. 64, fig. 9) is a peculiar variant which has spirals around the umbilicus but absent on the latero-venter. Its distinctive feature, however, lies in the periodic development of strengthened transversals at 22 mm. shell diameter which persist up to the maximum diameter of the specimen (25·5 mm.). This is the type of ornament characteristic of *G. radiatus* sp. nov. but in that species the periodically strengthened transversals succeed a dominant spiral ornament, whereas in this variety there is no stage of dominant spirals in the ontogenetic development of the ornament.

Apart from the first and last described variants we may regard these varieties as marking transitional stages in the development of a *G. crenistria* type of ornament into a *G. striatus* type. The earliest stages are very similar to *G. crenistria* in the presence of crenulate transversals and absence of spirals but the course of the transverse ornament serves to distinguish the two. Then spirals appear, first around the umbilicus and then on the latero-venter and venter. Finally they occur weakly on the flanks. This is the typical condition. The spirals finally strengthen to become as strong as the transversals when the test assumes a reticulate ornament, but the spirals never dominate the transversals as in typical *G. striatus*.

Comparisons with other species. Bisat (1952, pl. 1, fig. 4) figured a specimen (G.S.M. 85641) under the name of *Goniatites crenistria* late form from horizon Co5 from Cowdale Clough, Barnoldswick, Yorkshire, which occurred 10 feet below the *G. falcatus* bed. In the presence of spirals around the umbilicus, this specimen resembles *G. concentricus* but differs in the straightness of the transversals as they cross the flanks, there being neither umbilical bow nor any sign of a lingua at a shell diameter of 30 mm. In this respect Bisat's specimen might be expected to be an earlier form than *G. concentricus*. Moreover, the size of the umbilicus, about 25 per cent. of the shell diameter, is greater than that of *G. concentricus*.

Bisat (1957, pp. 16–19, pl. 3, figs. 1–3, 5–7; text-figs. 1–6) described *Goniatites warslowensis* from beds presumed to be above the horizon of *G. falcatus* and commented on the similarity between the ornament of this species and Kobold's *G. intermedium*. But the spirals seem to be stronger in *G. concentricus* and a notable difference lies in the hyponomic sinus which is absent at 25 mm. diameter in *G. warslowensis* but already developing at 10 mm. in *G. concentricus*.

Goniatites striatus (J. Sowerby)

Plate 65, figs. 1–3

Ammonites striatus Sowerby 1814, p. 115, pl. 53, fig. 1.
Paraglyphioceras striatus Brüning 1923, p. 265.

Goniatites striatus Bisat 1924, p. 74.
Glyphioceras striatum striatum Schmidt 1925, p. 568.
Goniatites striatus Bisat 1934, p. 301, pl. 18, fig. 1; pl. 19, figs. 1, 2; pl. 21, fig. 1.
Goniatites striatus Delépine 1940, pp. 79–80, pl. 5, figs. 16–17.
Goniatites striatus Delépine 1941, p. 67, pl. 4, fig. 69; pl. 5, figs. 1, 2.

Holotype. B.M. 43870 (figured Bisat 1934, pl. 19, fig. 1). From 'Derbyshire'; exact location and horizon not known.

Horizon. Viséan, P_{1b} in England and Ireland. $III\beta_{1-5}$ in Germany (*fide* Kobold 1933).

Diagnosis. *Goniatites* in which dominant transverse striae in young give place to dominant spirals. Transverse elements of shell ornamentation reappear only at diameters greater than 60 mm. Suture line with wide lateral lobe and median saddle 50 per cent. of depth of ventral lobe.

Description of holotype. Dimensions: diameter 41 mm., thickness 25 mm. (T/D % = 63), umbilicus plus inner area 5 mm. (U/D % = 13). The holotype is incomplete terminating across a septum. Some seven-eighths of the outer whorl is testiferous and shows spirals spaced at intervals of 0·3 mm. in the middle of the flanks at 30 mm. shell diameter. The transversals are very weak and the shell at 39 mm. diameter is ornamented by spiral striae almost exclusively. There appear to be no constrictions. The suture line, figured by Bisat (1934, pl. 19, fig. 2), is characterized by having a very wide lateral lobe. The course of the transversals departs very slightly from the radial direction across the flanks. At 33 mm. a very shallow lingua (less than 1 mm.) appears.

Ontogeny. A series of specimens from Co. Leitrim and Derbyshire enable the ontogenetic development to be investigated. G.S.M. Zl 4055 (Pl. 65, fig. 3) shows the dominant transversals spaced at about 7 per mm. at a shell diameter of 10 mm. in the centre of the venter. These are almost radial on the flanks bending forward at the latero-venter into a slightly dented, forwardly directed bow over the venter. There are faint spirals around the umbilicus. On specimen Zl 3832 (Pl. 65, fig. 2) the crenulate transversals are still dominant at 21 mm. shell diameter being spaced at 2 per mm. in the centre of the venter. The spirals have strengthened but are still confined to the vicinity of the umbilicus. The transversals bend slightly forward on leaving the umbilicus, passing radially up the flanks and swinging back gently to form a very shallow hyponomic sinus. Specimen Zl 3133 shows that at 26 mm. shell diameter the spiral ornament has become dominant and extends all over the shell. G.S.M. 53552 from Jack Bank Quarry, Derbyshire, has a few transversals slightly accentuated and their course at 24 mm. diameter is almost radial on the flanks without a lingua and with a hyponomic sinus of 2½ mm. depth. The spirals remain dominant up to diameters between 60 and 70 mm. Thus G.S.M. 53553 shows only faint traces of transversals even at 67 mm. diameter. In G.S.M. 57922, also from Jack Bank Quarry, however, the transversals reappear at about a diameter of 64 mm. and gradually strengthen until at 81 mm. they are again the dominant element in the shell ornament. These large specimens show that the length of the body chamber is about 380°. Constrictions are not common and have been seen on one specimen only, namely Zl 4053 which shows a constriction on the internal mould at 27 mm. diameter.

Discussion. According to Bisat (1934) the species differs from *G. maximus* Bisat in that the latter is generally stouter. T/D% averages 63 in *G. striatus* and 75 in *G. maximus*.

Moreover, the median saddle of the suture line is less elevated in *G. maximus* being 40 per cent. of the depth of the ventral lobe as against 50 per cent. in *G. striatus*. The ornament is closely similar.

Goniatites spirifer Roemer

Plate 66, figs. 1, 3, 4

Goniatites spirifer Roemer 1850, p. 51, pl. 8, fig. 16.
Goniatites striatus Phillips 1836, pl. 19, fig. 1.
Goniatites striatus Smith 1903, pl. 10, fig. 11.
Glyphioceras crenistria var. *praestriata* Schmidt 1925, p. 566, pl. 21, fig. 2.
Glyphioceras spirifer Haubold 1930, p. 79.
Glyphioceras striatum spirifer Kobold 1933, pp. 489–90, pl. 22, figs. 5, 6.
Goniatites spirifer Hudson and Cotton 1945, p. 265, text-fig. 2.

Holotype. Mining Institute, Clausthal No. 389, figured by Kobold 1933, pl. 22, fig. 6: from 'Posidonomyenschiefer', near Lautenthal, Harz Mountains, Germany.

Horizon. Lower Lautenthal Shales, IIIα/β to IIIβ_3, in Germany (*fide* Kobold 1933). Viséan, P_{1b} in England and Ireland.

Diagnosis. *Goniatites* of the *G. striatus* stock developing a persistent stage of ornamentation characterized by thin, widely-spaced grooves following the direction of the peristome.

Description. The species agrees with the general description of *G. striatus* except for the appearance of widely-spaced transverse grooves cutting across the spirals and forming strap-like bands of test between. This type of ornamentation (*spirifer*-stage) is seen to succeed the *striatus*-stage of ornamentation at various diameters and in varying degrees of perfection in different specimens. Moreover, it normally precedes the typical *radiatus*-stage ornament in the ontogeny of *G. radiatus* (Pl. 67). In order to make more precise a species which until now has been very poorly known and figured from poor shale impressions, we restrict it to shells in which the characteristic ornament appears before 50 mm. shell diameter and persists until fully grown. Large specimens of *G. striatus* with a terminal short, feeble *spirifer*-stage will still be called *G. striatus*. Specimens in which the *spirifer*-stage is followed by a *radiatus*-stage which occupies a considerable portion of the termination of the shell will be called *G. radiatus*. For examples in which the *spirifer*-stage is followed by a short, poorly developed *radiatus*-stage the best name would seem to be *G. spirifer* mut. towards *radiatus*.

Remarks. Information is to hand that German palaeontologists are now inclined to place the range of *G. spirifer* entirely *below* the *G. crenistria* zone, P_{1a}. This seems to us very doubtful since Roemer gave the horizon of the holotype as the 'Posidonomyenschiefer near Lautenthal', and Kobold has found comparable material with the same state of preservation near Lauthenthal in this formation and dates the beds as IIIβ_1. It seems that confusion exists between the true *G. spirifer* (from above P_{1a}) and homoeomorphs belonging to the *G. maximus* stock (such as *G. struppus* sp. nov. [see p. 395]; Bisat 1934, pl. 22, figs. 3 and 4) which occur below P_{1a} in England.

On the basis of the figures given by Phillips (1836) and J. P. Smith (1903) their specimens ought to be referred to *G. spirifer* rather than *G. striatus*. The constrictions mentioned by Phillips and shown in his figure are, in our experience, unusual in members of the *G. striatus* stock. Foord and Crick (1897, p. 168) mention ornament of the type here referred to as the *spirifer*-stage in certain specimens identified by them as *G. striatus*, but such ornament is absent from the holotype of *G. striatus* (see Bisat 1934, pl. 19, fig. 1).

Goniatites radiatus sp. nov.

Plate 67, fig. 1; Plate 68, figs. 1, 2, 4, 5

Goniatites falcatus Delépine 1940, pl. 5, figs. 13, 14.

Holotype. G.S.M. Zl 3129 (Pl. 68, fig. 5), Dough Mountain, Co. Leitrim, Ireland.

Horizon. Viséan, P_{1b}.

Diagnosis. *Goniatites* of the *G. striatus* stock in which test ornament of the *G. striatus* type is succeeded by a transient stage of *G. spirifer* type and finally by ribs and grooves which interrupt the spiral ornament as in *G. falcatus* but which lack the marked forward umbilical bowing of that species.

Dimensions (in mm.)

	Diameter	*Thickness*	*T/D%*	*Umbilicus plus inner area*	*U/D%*
Zl 3129	71·1	38·0	49	8	11
	70·0	35·0	50	7½	11
	56·0	35·0	63	6½	12
	40·2	28·2	70	4½	11

Description. The ontogenetic development of the test ornament is well shown in the specimen (G.S.M. Zl 7330) figured on Pl. 67. In the earliest portion of the ornament seen on the last whorl the strength of the spirals and the transversals is equal and the reticulate ornament characteristic of *G. concentricus* in evidence. The transversals gradually lose strength and the spirals become dominant. Then for about a quarter of a whorl the ornament is in the *striatus* condition. Marked grooves, distantly spaced, then appear and for a short distance the *spirifer* type of ornament is assumed. Between these distant grooves appear others which at first do not extend down to the umbilical edge. Finally, relatively closely-spaced ribs interrupting the continuity of the spirals as in the *falcatus* ornament (but with a more rectilinear course over the flanks) constitute the adult ornament.

The changes in whorl shape can be seen in the sectioned specimen (Pl. 68, fig. 4) where the cadicone stage is seen to end at the 6th whorl, after which the whorl height rapidly increases relative to the thickness. This contrasts with *G. falcatus* where the cadicone stage persists up to the 8th whorl. The umbilicus slowly decreases from 15 per cent. of the diameter at the end of the 6th whorl to 10 per cent. of the diameter at the 10th whorl. In these particulars it resembles *G. concentricus* or *G. striatus* rather than *G. falcatus*.

Discussion. Although the essential continuity of the *concentricus*, *striatus*, *spirifer*, and *radiatus* ornamentation patterns can be easily demonstrated, the transition from the last to *falcatus* is not so commonly seen. In the specimen figured on Pl. 68, fig. 2, the course of the transversals shows an approach to those of *G. falcatus* in the later part of the last whorl.

Goniatites falcatus Roemer

Plate 65, fig. 5; Plate 68, fig. 3; Plate 69, figs. 1–6

Goniatites falcatus Roemer 1850, p. 50, pl. 80, figs. 11, 12.
Glyphioceras subreticulatum Frech 1899, pl. 46*a*, fig. 6.
Glyphioceras striatum falcatum Schmidt 1925, p. 569, pl. 21, fig. 7; *non* pl. 23, fig. 18.
Glyphioceras striatum falcatum Haubold 1930, p. 90.
Glyphioceras striatum falcatum Kobold 1933, pp. 420–1.
Goniatites falcatus Moore 1936, p. 180.

Holotype. Mining Institute, Clausthal No. 392 (Pl. 68, fig. 3), from 'Posidonomyenschiefer', Lautenthal, Harz Mountains, Germany.

Horizon. Viséan, P_{1b} in England and Ireland. $III\beta_{3-4}$ in Germany (*fide* Kobold 1933).

Diagnosis. Goniatites with strong doubly-bowed transversals and hyponomic sinus. Transversals rib-like and interrupting spiral ornament. Relatively narrow first lateral lobe and tall, pointed first lateral saddle.

Dimensions (in mm.)

	Diameter	*Thickness*	*T/D%*	*Umbilicus plus inner area*	*U/D%*
Zl 4033	49·0	30·6	63	9·5	19
	48·1	32·0	67	8·7	18
	47·3	29·6	63	8·1	17
Zl 3881	43·6	29·3	67	8·5	20
	37·0	24·5	67	5·3	14
Zl 3882	33·7	25·2	75	6·3	19
Zl 3762	31·3	23·1	74	6·2	20

Description of holotype. The holotype (Pl. 68, fig. 3) is an imperfect specimen of which only the right side is preserved and the suture line is not visible. The estimated diameter is 51 mm. with an umbilical width of 18 per cent. In the strength and direction of the transverse ornament it agrees perfectly with the Irish specimens described below.

Description of Irish specimens. Typically the species has a relatively stout shell but, as can be seen from the above dimensions, there is some variation. Thus, between 30 and 50 mm. shell diameter, the ratio T/D% ranges between 62 and 74. The umbilicus is fairly wide but again variable, being 14–20 per cent. of the shell diameter.

The most distinctive feature of the species is the ornament consisting of strong transversals, of rib-like strength, with a typical cross-section in the line of the plane of symmetry. There is a steep forward rise to the point of inflexion and a gentle backward slope to the next 'rib'. The transversals interrupt the spiral ornament which is impressed only on the 'dip slope' of the rib except that in the region around the umbilicus the spirals are more continuous (Pl. 69, fig. 5). On some well-preserved examples the spirals may dent the forward edge of the rib, producing a crimped effect. On leaving the umbilicus, the transversals bend markedly forward and then swing gently but decidedly backwards to form a sinus situated well up the flanks. Thence they proceed to describe a very small lingual bow before passing over the venter to form a hyponomic sinus which is 1 mm. deep at 30 mm. shell diameter and between 4½ and 6½ mm. deep at 45–49 mm. shell diameter.

The suture line is shown in text-figs. 2, 3. The narrowness of the first lateral lobe is in contrast to that of *G. striatus* (q.v.).

Internal characters. A specimen (Pl. 65, fig. 5) sectioned along the median plane is entirely septate and shows 8⅞ whorls. The density of septation is as follows: whorl no. 1 contains 5 septa; whorl 2 has 8 septa; whorl 3 has 9 septa; whorl 4 has 13 septa; whorl 5 has 16 septa; whorl 6 has 20 septa; whorl 7 has 17 septa; whorl 8 has 17 septa; whorl 9 has 20 septa (estimated). The septal necks are all retrosiphonate to the end. The main feature shown by a section at right angles to the plane of symmetry (Pl. 69, fig. 1) is the relative persistence of the cadicone stage. Thus it is only in the last visible whorl (the 9th) that the whorl height begins to increase relative to the width. As compared with other members of the *G. striatus* stock, there is a persistence of a whorl shape characteristic of the young of the *striatus* group into the adult of *G. falcatus*.

Discussion. The specimen figured by Delépine (1941, pl. 4, fig. 10) and attributed to *G. falcatus* has much weaker ornament than typical *G. falcatus* and would be attributable to *G. spirifer* were it not for the presence of a decided umbilical bow on the transversals. The two Belgian specimens figured by Delépine (1940, pl. 5, figs. 13–15) are also not typical of *G. falcatus*. The original of the specimen shown in figs. 13 and 14 seems to be *G. radiatus* sp. nov., and that of fig. 15 to be near to *G. spirifer*. The specimen figured by Schmidt (1925, pl. 23, fig. 18 reproduced here as Pl. 65, fig. 4), which is 42 mm. in diameter, is unusual, as Schmidt pointed out, in showing the early part of the last whorl bearing typical *striatus* ornament succeeded abruptly (with ⅛ whorl) by typical *falcatus* ornament.

GENERAL DISCUSSION

As previously indicated we have not found the species just described succeeding each other in any definite stratigraphical order, although the possibility of different species forming the modal type at successive horizons is mentioned. Thus although ontogenetically the sequence *concentricus—striatus—spirifer—radiatus—falcatus* can be demonstrated we are not able to claim that the group evolved palingenetically in this way. It would appear from the succession given by Kobold, together with his estimates of the relative abundance of the three species recognized by him, that *G. spirifer* preceded *G. striatus*. We have not been able to repeat the bed-by-bed collecting done by Kobold and until this is done it might be thought presumptuous to challenge his conclusions; nevertheless, on the basis of our ontogenetic studies we would be surprised if in fact the maximum of *G. spirifer* did precede that of *G. striatus*. It is, however, to be admitted that Hudson and Cotton (1945) recorded a succession of members of this group in the Alport borehole and identified the lowest members of it as *G. spirifer*. But they (contrary to Kobold) found forms identified as *G. falcatus* succeeding it and preceding the appearance

EXPLANATION OF PLATE 64

Figs. 1–3, 5–8. *Goniatites concentricus* sp. nov., Dough Mountain, Co. Leitrim, Ireland. 1, Nucleus of a striatoid goniatite attributed to this species showing appearance of spirals round the umbilical edge, G.S.M. 87225, ×5. 2, Same specimen, ventral view with incipient spirals at the latero-venter and commencement of hyponomic sinus, ×5. 3, Variant with fine transverse ornament, G.S.M. 87224, ×2. 5, Section almost in the median plane (the portion above the line is almost exactly median), G.S.M. Zl 7337, ×2. 6, Transverse section, the plane of section passes slightly in front of the protoconch and the innermost circle is the first whorl, not the protoconch. 7, Holotype, G.S.M. 87221, ×2. 8, Variant lacking spirals on latero-venter, G.S.M. 87222, ×2.

Fig. 4. *Goniatites* sp., Dough Mountain, Co. Leitrim, Ireland. Transitional from *G. concentricus* to *G. striatus*, G.S.M. 87220, ×2.

Fig. 9. *Goniatites* aff. *concentricus* sp. nov., Dough Mountain, Co. Leitrim, Ireland. Accentuation of transversals near peristome as in *G. radiatus* sp. nov., G.S.M. 87223, ×2.

EXPLANATION OF PLATE 65

Figs. 1–3. *Goniatites striatus* (J. Sowerby), Dough Mountain, Co. Leitrim, Ireland. 1, Faint transversals visible in early part of last whorl but later dominated by spirals, G.S.M. Zl 7316, ×2. 2, Note dominant transverse ornament but spirals appearing round umbilicus, G.S.M. Zl 3832, ×2. 3, Young specimen showing transverse ornament on venter, spirals absent, G.S.M. Zl 4055, ×2.

Fig. 4. *Goniatites falcatus* Roemer var., copy of Schmidt 1925, pl. 23, fig. 18. Typical *striatus* ornament rapidly succeeded by typical *falcatus* ornament, ×1½.

Fig. 5. *Goniatites falcatus* Roemer, Dough Mountain, Co. Leitrim, Ireland, median section.

Fig. 6. *Goniatites concentricus* sp. nov., River Ribble, Dinckley, Lancashire. Manchester Museum LL 256, ×2½, figured Moore 1936, pl. 3, fig. 3.

EXPLANATION OF PLATE 66

Figs. 1, 3, 4. *Goniatites spirifer* Roemer, Dough Mountain, Co. Leitrim, Ireland. 1, Note the appearance of widely-spaced transverse grooves at 48 mm. shell diameter, G.S.M. Zl 7325, ×2. 3, G.S.M. Zl 7328, ×2. 4, G.S.M. Zl 7327, ×2.

Fig. 2. *Goniatites sp.*, Dough Mountain, Co. Leitrim, Ireland. Note *striatus* ornament succeeded by a short *spirifer* stage and finally *radiatus* ornament. G.S.M. Zl 7326, ×2.

EXPLANATION OF PLATE 67

Fig. 1. *Goniatites radiatus* sp. nov., Dough Mountain, Co. Leitrim, Ireland. Showing succession of test ornamentation in which the *concentricus*, *striatus*, *spirifer*, and *radiatus* types are seen in that order in the last whorl. G.S.M. Zl 7330, ×4·2.

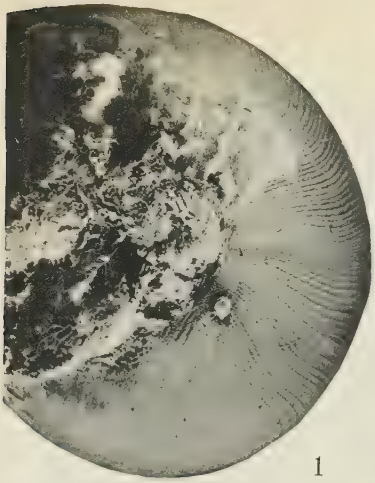
EXPLANATION OF PLATE 68

Figs. 1, 2, 4, 5. *Goniatites radiatus* sp. nov., Dough Mountain, Co. Leitrim, Ireland. 1, G.S.M. Zl 7331, ×1. 2, Showing development of umbilical bow in transverse ornament near aperture, G.S.M. Zl 7329, ×1. 4, Median section, G.S.M. Zl 7332, ×1. 5, Holotype, G.S.M. Zl 3129, ×1.

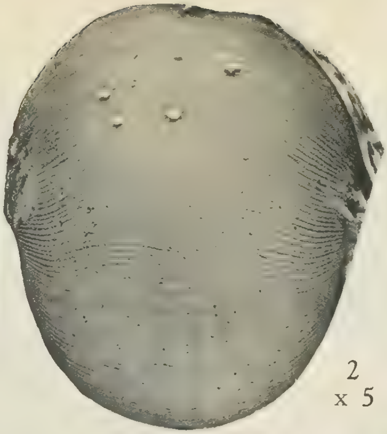
Fig. 3. *Goniatites falcatus* Roemer, holotype, Mining Institute of Clausthal collection No. 392, ×1½, Posidonomyenschiefer, Lautenthal, Harz Mountains, Germany.

EXPLANATION OF PLATE 69

Figs. 1–6. *Goniatites falcatus* Roemer, Dough Mountain, Co. Leitrim, Ireland. 1, Median section, G.S.M. Zl 7333, ×2. 2, Note strong sinuous transversals and spirals continuous round the umbilicus but interrupted higher on the flanks; also narrow lateral lobe of the suture line, G.S.M. Zl 3762, ×2 (see also fig. 6). 3, G.S.M. Zl 3881, ×2. 4, Same specimen as fig. 3, venter, note depth of hyponomic sinus, ×2. 5, Details of spiral ornament of specimen figured in fig. 3, note shape of transverse ribs and interrupted spirals, ×6·7. 6, Ventral view of same specimen as fig. 2, note tall external saddle of the suture line with pointed tip, ×2·4.



1
x 5



2
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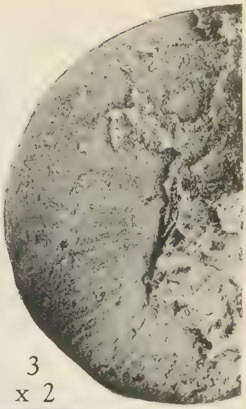
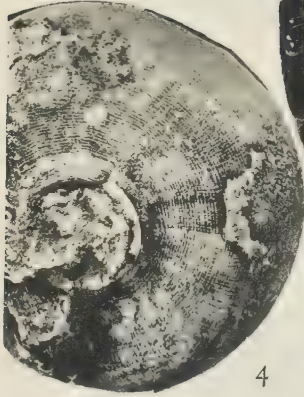


3
x 2



4
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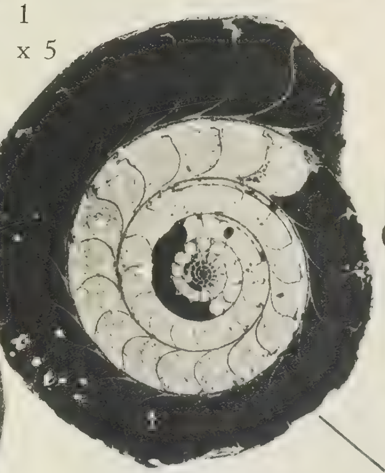
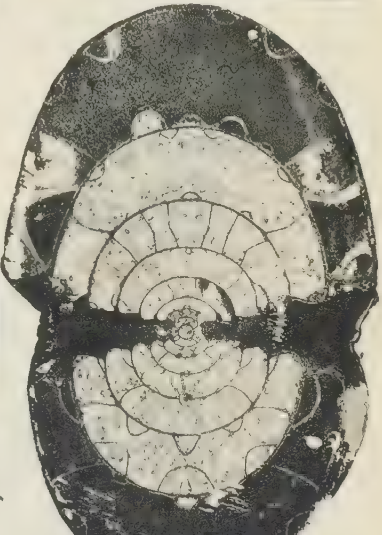


5 x 2



6
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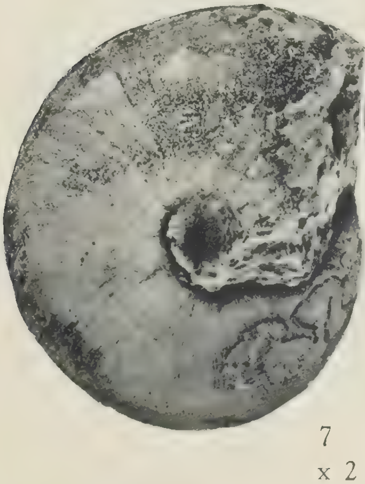
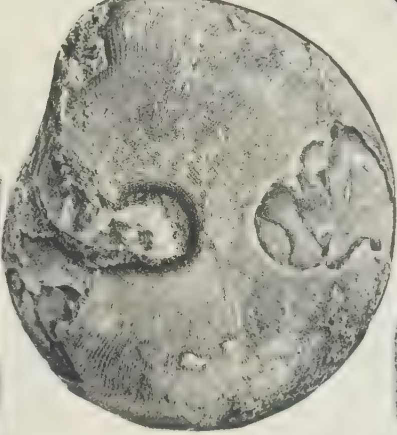
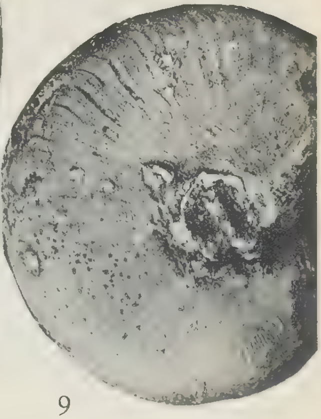


7
x 2

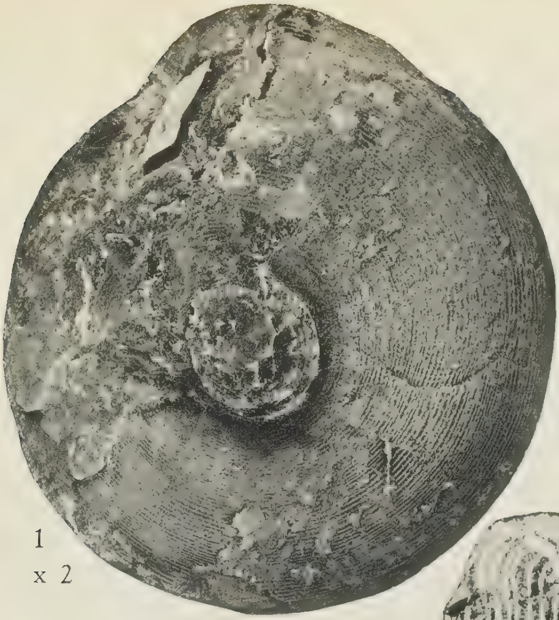


8
x 2



9
x 2

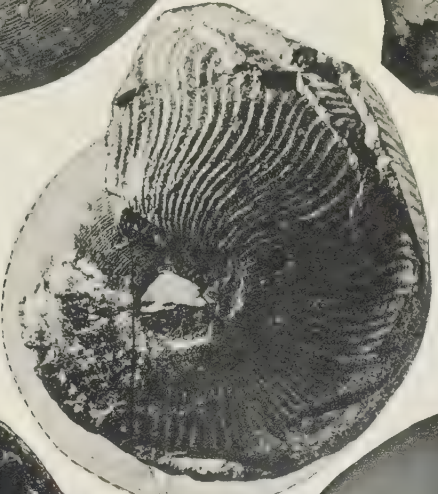
HODSON and MOORE, *Goniatites concentricus* sp.nov.



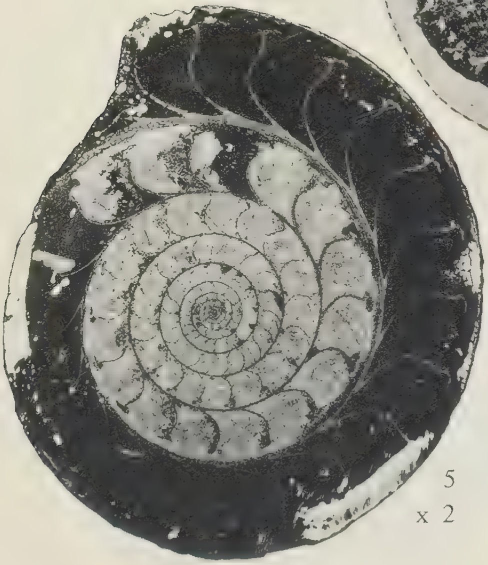
1
x 2

2 x 2

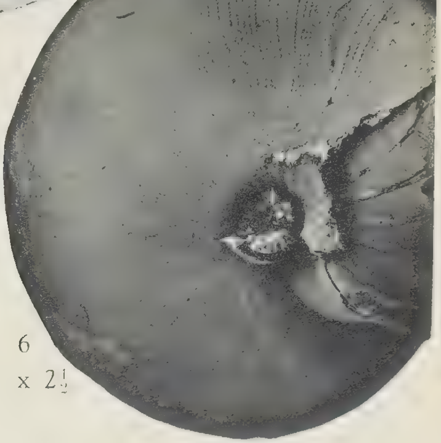
3
x 2



4
x 1½



5
x 2



6
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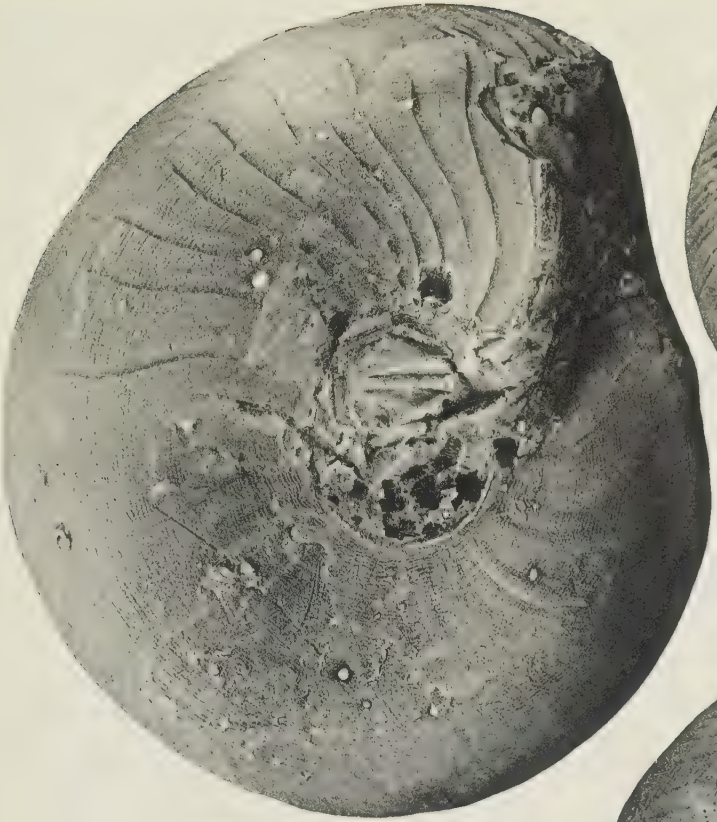
HODSON and MOORE, *Goniatites spp.*



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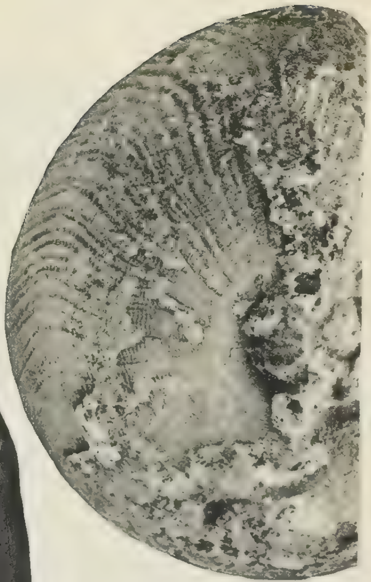

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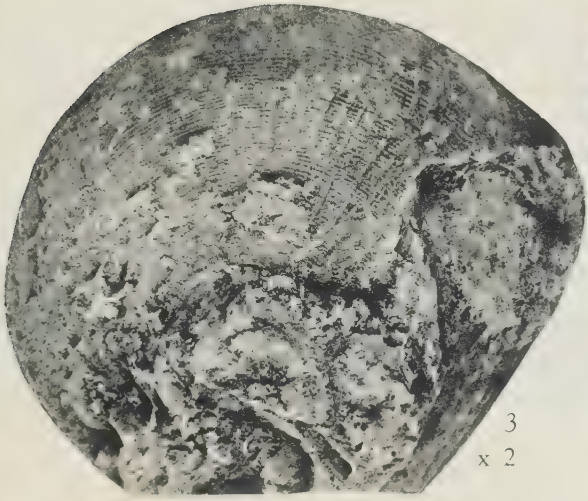

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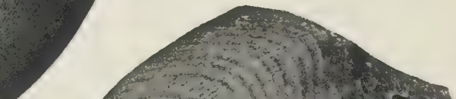

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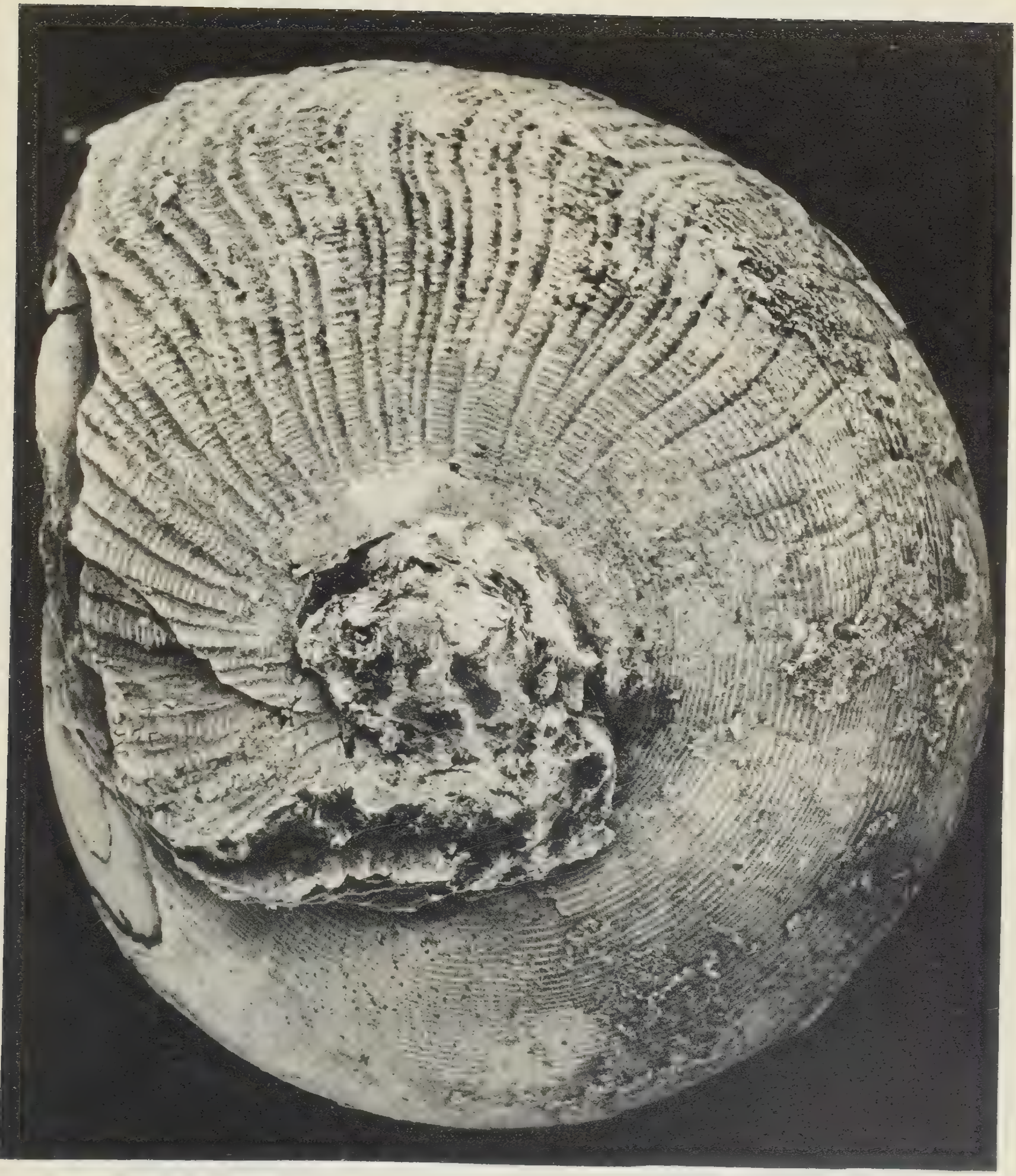

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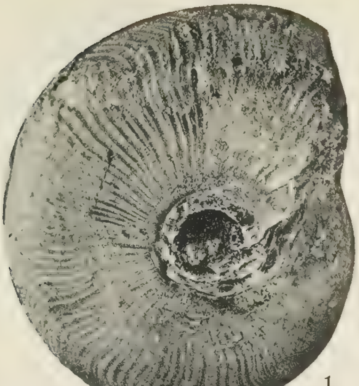
HODSON and MOORE, *Goniatites radiatus* sp. nov.



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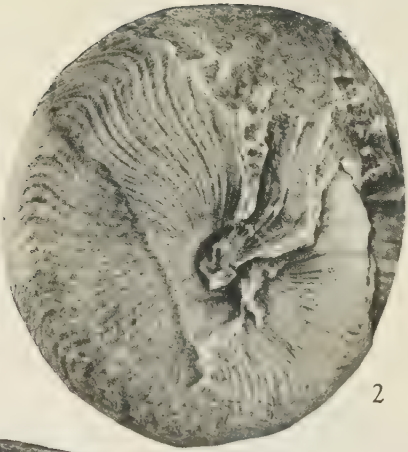

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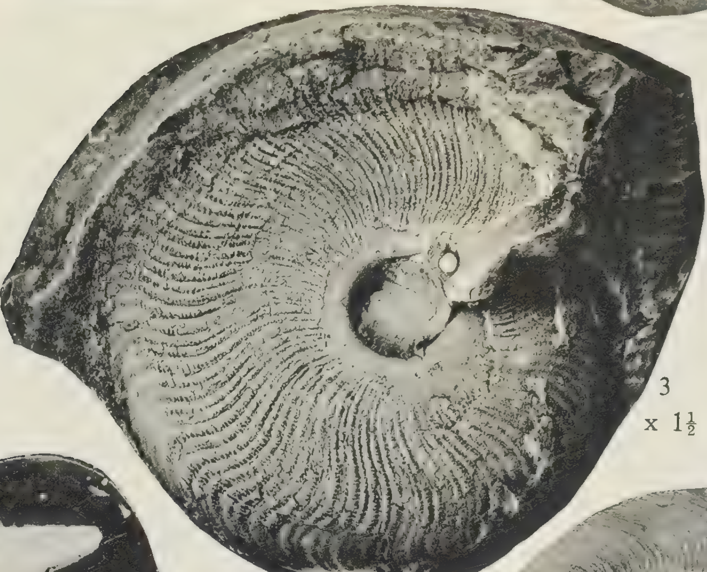
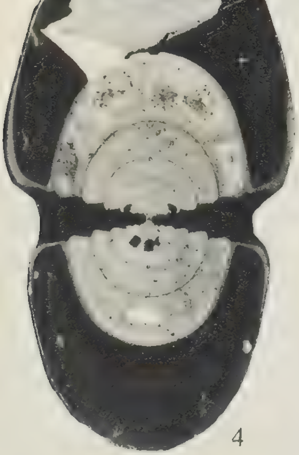


3

x 1½



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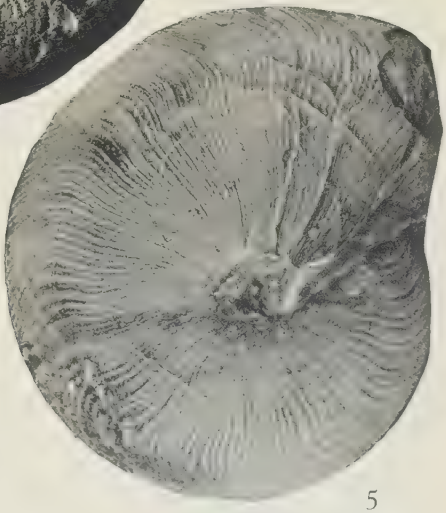
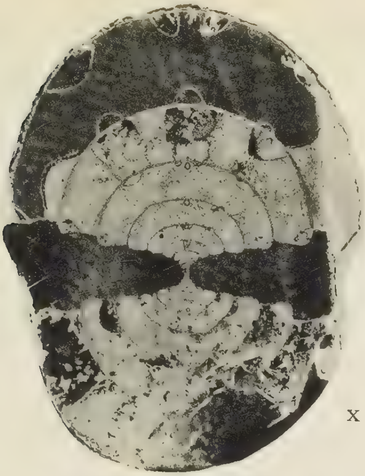


5

HODSON and MOORE, *Goniatites spp.*



1
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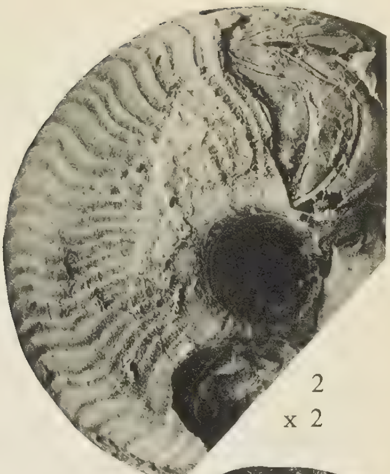

2
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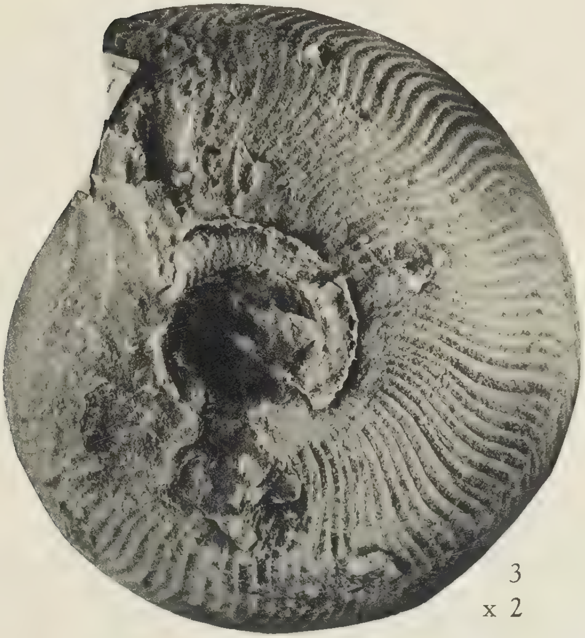

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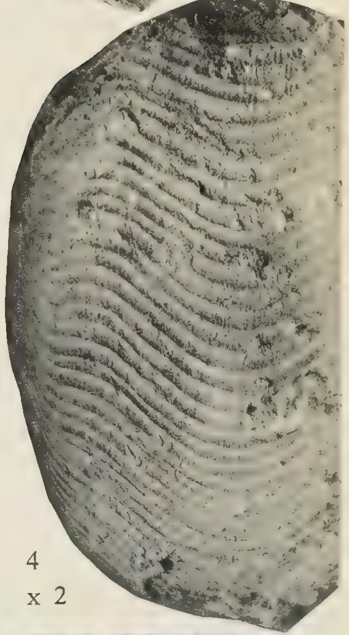

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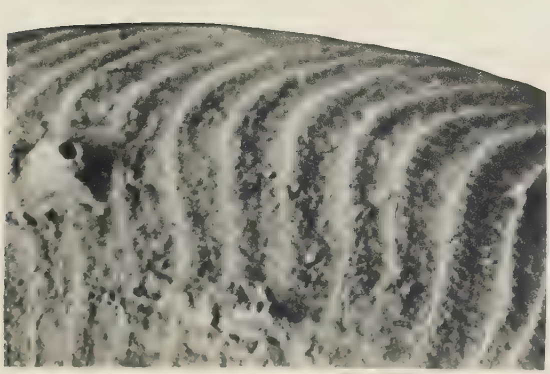
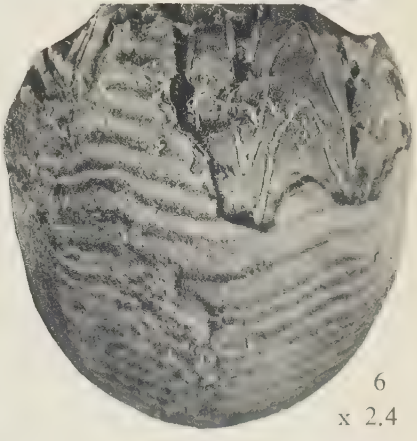


5
x 6.7



6
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HODSON and MOORE, *Goniatites falcatus* Roemer

of *G. striatus*, although ultimately overlapping it. It must then be admitted that the ontogenetic appearance of the different ornaments characterizing the species here described cannot be shown to be paralleled by their stratigraphical order and indeed such evidence as exists is contrary to the idea.

From a stratigraphical point of view it is also important to describe what appears to be the operation of a similiar trend in the ornament stages upon an earlier goniatite stock in the B_2 zone, producing forms which are, so far as the test ornament is concerned, homeomorphic with some of the species described above. These earlier forms belong to the *Goniatites hudsoni—maximus* stock. Bisat (1934) described this group and derived the interrelationships of the forms known to him at the time. Apparently the earliest species is *G. antiquatus* Bisat with faintly crenulate transversals. *G. hudsoni* has strongly crenulate transversals with a few spirals round the umbilical margin. Both these species may be regarded as in the *crenistria*-stage when adult. *G. wedberense* Bisat is also in this stage up to a shell diameter of 25 mm., but at a greater size becomes reticulate, i.e. features the *concentricus*-stage. *G. maximus* Bisat persists in the *crenistria*-stage up to 18 mm. diameter. Between 18 and 25 mm. the ornament is in the *concentricus*-stage. Above this diameter the spirals become dominant, at first around the umbilicus, then on the flanks, and finally at 32 mm. diameter they cover the complete shell. In the typical form this, the *striatus*-stage, persists for the rest of its growth, but in *G. maximus* var. c. Bisat (1934) at 45 mm. diameter the thin grooves characteristic of the *spirifer*-stage appear. It is here proposed to name this variety *Goniatites struppus* sp. nov. (holotype G.S.M. 53549, figured Bisat 1934, pl. 22, figs. 3, 4, p. 299, from Black Hole, Malham, Yorkshire, B_2 zone). There appear to be no homeomorphs of *G. radiatus* and *G. falcatus* in the B_2 zone. The discrimination between the known homeomorphs from the B_2 and P_1 zones is very difficult and would require well-preserved material. It is a subject of future investigation.

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PROBABLE CIRRIPEDE, PHORONID, AND ECHIUROID BURROWS WITHIN A CRETACEOUS ECHINOID TEST

by K. A. JOYSEY

ABSTRACT. Natural flint casts representing several different types of burrows were found within the thickness of the test of a Chalk echinoid. They have been compared with the burrows inhabited by various living animals. It is concluded that they indicate the probable presence of an acrothoracican cirripede, a phoronid, and an echiuroid, and the possible presence of a lamellibranch, polychaet and other 'worms', and sponges. No new names are proposed for these burrows because they cannot be regarded as parts of organisms.

THE burrows described in this paper were found within the thickness of the test of a single specimen of the echinoid *Echinocorys*, which was collected from a beach boulder, derived from the Chalk of Culver Cliff, Isle of Wight. The fossil was almost completely filled with flint and completely enclosed in flint, but the echinoid test itself was not silicified.

With the intention of preparing a perfect internal cast of the *Echinocorys*, the flint was broken off the outside and the specimen immersed in hydrochloric acid in order to dissolve the test. When about half of the thickness of the test had been removed the burrows were revealed as natural casts in flint adhering to the remaining inner part of the test. In order to preserve the burrows the original plan to dissolve away the whole of the test was abandoned, and subsequently they were further prepared by dropping on small amounts of dilute hydrochloric acid from a pipette.

DESCRIPTION AND INTERPRETATION

Due to their method of preparation, the burrows have a misleading resemblance to certain adherent organisms, and so it must be stressed that the structures shown on Pl. 70 are casts of excavations. Although the burrows were present before fossilization there is no direct evidence to indicate whether they were constructed before or after the death of their host.

For reference purposes a letter has been allocated to each of the seven different kinds of cast (A–G), but not all of these structures are burrows. They have been compared with figures and descriptions of burrows inhabited by living plants and animals, but all of them are considerably larger than the excavations that are attributed to plants (Bornet and Flahault 1889).

A. These are casts of the pore-pairs in the ambulacral plates of the echinoid (Pl. 70, figs. 2, 3). They now project from the surface of the specimen like rows of miniature factory-chimneys, and the tops of the tallest chimneys indicate the level of the original outer surface of the echinoid test.

B. There is only a single example of this type of burrow (Pl. 70, fig. 1). It commences with a subcircular aperture on the outside of the test, from which it gradually increases in diameter along the greater part of its length, and then narrows slightly in the final

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stage. It is unbranched, but there are three sharp changes in direction, each of which appear to avoid intersection with another burrow of a different type.

At the present time a burrow of this kind could possibly be inhabited by a small lamellibranch comparable with *Gastrochaena dubia* (Pennant), but more probably by a polychaet worm comparable with *Dodecaceria concharum* Oersted (= *Heterocirrus saxicola* Grube) or *Potamilla reniformis* (Müller) (= *Sabella saxicava* Quatrefages), all of which are reviewed by McIntosh (1868, 1908).

Similar burrows in brachiopod shells have been figured from the Devonian of North America (Clarke 1921, figs. 78–82, fig. 101) and from the Permian of Australia (Teichert 1945, pl. 3, fig. 1), and in each case have been attributed to worms.

C. There is only a single example of this type of burrow (Pl. 70, fig. 1) which has a narrow entrance tunnel and an expanded inner chamber. The early part of the entrance tunnel has not been fully exposed, but it appears that the aperture was on the inner side of the echinoid test. The far end of the chamber is divided into several lobes, which appear to represent several unsuccessful attempts to pass above burrow B, which occupies the greater part of the thickness of the test.

At the present time similar burrows are inhabited by echiuroid worms comparable with *Thalassema neptuni* Gaertner, the shape of the burrow reflecting the shape of the worm. Farran (1851) stated that this species 'accurately filled' its burrows within a limestone pebble. Jameson (1899) stated that it generally inhabited burrows which had been made by the lamellibranch *Saxicava*. Although it appears to be uncertain whether echiuroids can entirely construct their own burrows, Lankester (1868) noted that *Bonellia* inhabited cracks in rock which 'was to a certain extent excavated, thus fitting to the body of the worm'.

D. This branched burrow system appears to belong to a colonial organism (Pl. 70, fig. 3). There are several apertures to the outer surface of the test, which are joined by a burrow of approximately the same diameter as the apertures. Burrow D forms the greater part of the H-shaped system shown in fig. 3, but the entire left side of the H-shape is formed by an example of burrow E, which will be described below. The two different kinds of burrow system can be seen lying alongside one another in the top left branch of the H-shape. At the present time, burrows similar to D are inhabited by *Phoronis ovalis* Wright, which has been recorded burrowing within the shell of molluscs from Europe (Harmer 1917), Brazil (Marcus 1949), and New Zealand (Silen 1956).

E. This is the most extensive type of burrow system in the present specimen (Pl. 70, figs. 1, 2, and 3). The burrows run for long distances within the test, and are variable in diameter. Where branching occurs the two branches are sometimes of different diameter. The burrows often cross over one another and lie very close together but no unequivocal

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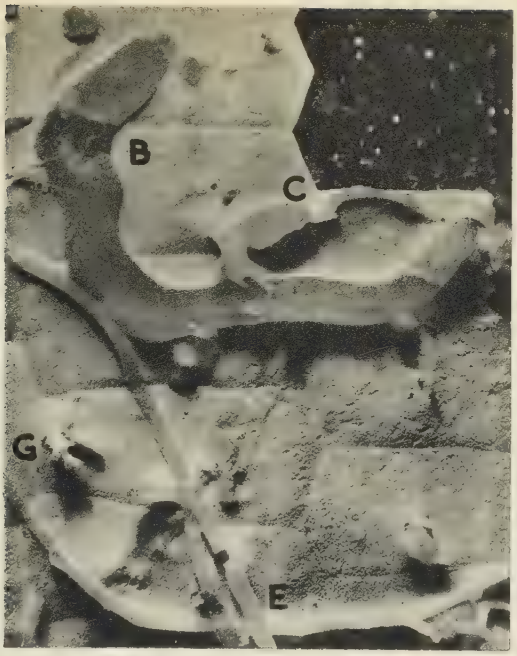
EXPLANATION OF PLATE 70

Figs. 1–3. Natural casts in flint of animal burrows within the thickness of the test of a single specimen of the echinoid *Echinocorys*, derived from the Chalk of Culver Cliff, Isle of Wight. The specimen has been prepared by dissolving away the outer surface of the test with hydrochloric acid. Figs. 1 and 2 are ×6; fig. 3 (oblique view), *c.* ×12. A, casts of pore-pairs of the *Echinocorys*; B, burrow possibly of a polychaet or lamellibranch; C, burrow probably of echiuroid; D, burrow probably of a phoronid; E, burrow possibly of 'worm' or sponge; F, burrow probably of acrothoracican cirripede; G, possible burrow of sponge or possible inorganic artifact.

Photographs by Mr. R. D. Norman.



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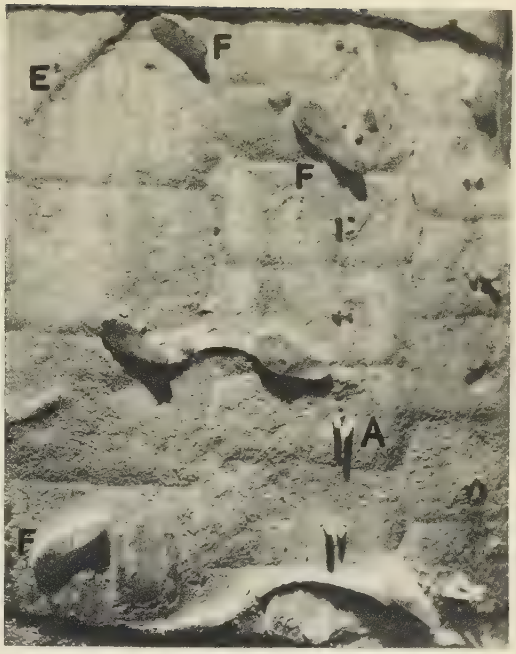

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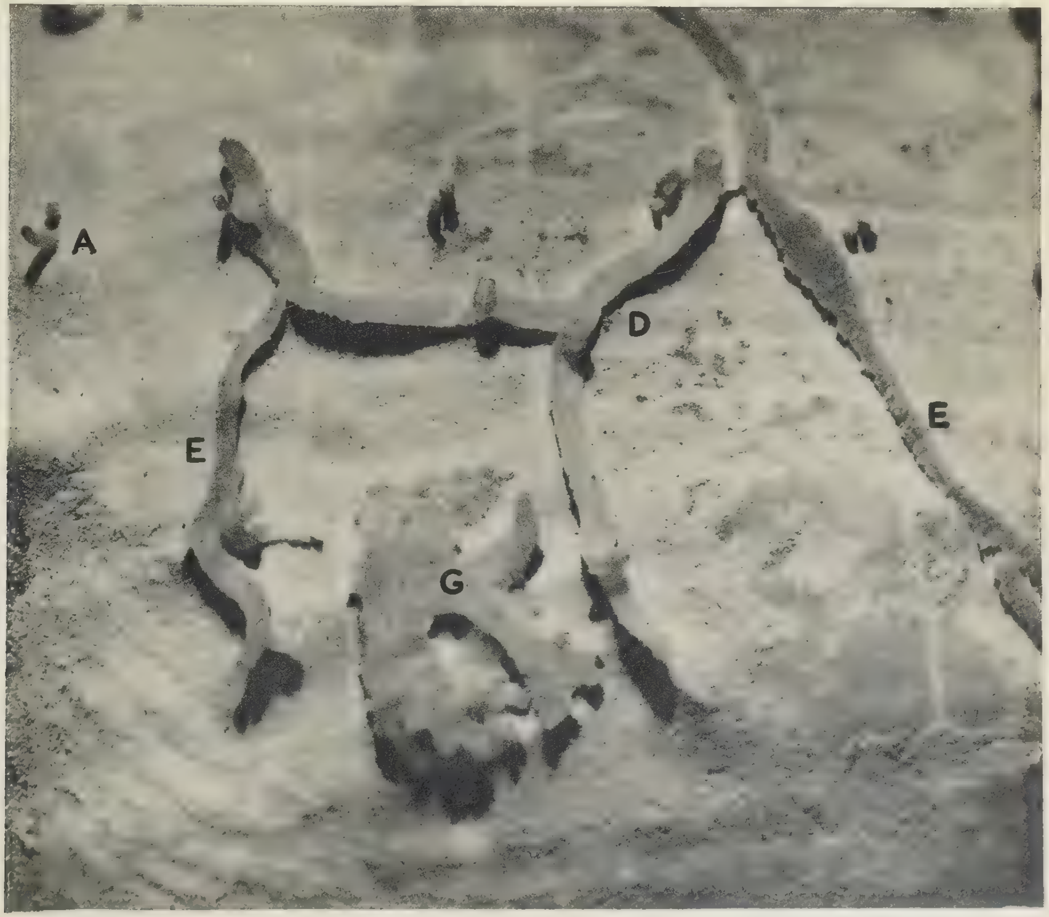

3 × 12

JOYSEY, Borings within an echinoid test

example of anastomosis has been observed. There are relatively few apertures (in comparison with burrow D), and the apertures sometimes have a smaller diameter than the tunnel from which they surface.

These burrows cannot yet be matched with those of any living organism. Similar burrows in brachiopod shells from the Permian of Australia (Teichert 1945) have been named *Conchotrema* and attributed to worms, but without any indication which of the several Phyla of worms is supposed to be responsible. Teichert (1945) states that the genus *Conchotrema* includes the Pennsylvanian form *Clionolithes canna* Price, which Clarke (1921) regarded as a sponge, and that it is similar to a Mississippian form which Girty (1915) regarded as a burrowing bryozoan.

Burrow system E bears little resemblance to living burrowing bryozoans which have been reviewed by Marcus (1938) and Silen (1947), but the other two hypotheses—sponge or 'worm'—appear to be equally possible interpretations.

F. These are the smallest individual burrows in the present specimen (Pl. 70, fig. 2). The six examples shown are part of a group, and there are seventeen individuals present in this one echinoid. Each of the burrows can be compared in shape with a shoe, although somewhat laterally compressed. The aperture of the burrow corresponds with the opening of a tightly laced shoe, being elongate oval in shape, almost slit-like. The space for the ankle is represented by an oval shaft which leads down into the inner chamber of the burrow.

At the present time burrows similar to F are inhabited by the cirripede *Alcippe lampas* Hancock, although the burrows of this species are relatively broader, and were originally compared with a Roman lamp (Hancock 1849*b*) rather than a narrow shoe. *Alcippe* is one of several genera of minute burrowing cirripedes included in the order Acrothoracica, reviewed by Gruvel (1905).

G. This structure is very variable, and may represent either a burrow system or an inorganic artefact (Pl. 70, figs. 1 and 3). It has an irregular arborescent and dendritic form, which may be centred on either the inner or the outer surface of the test. If these structures are casts of burrows they are comparable with some of the more irregular excavations at present inhabited by sponges (Hancock 1849*a*, Morris 1849, Topsent 1887). On the other hand, these structures may be the result of local replacement of the echinoderm test by silica penetrating from the surrounding flint.

DISCUSSION AND CONCLUSIONS

In order to identify the Cretaceous burrows it has been necessary to study descriptions of the burrows of living organisms. During this work it has emerged that (*a*) different kinds of burrow systems may be constructed by closely related organisms; (*b*) similar burrow systems may be constructed by unrelated organisms; (*c*) some organisms inhabit burrow systems which were originally excavated by a different organism (although the old burrow may be modified by the new occupant).

These observations on the burrows of living organisms are sufficient to explain the controversy which has frequently arisen over the identification of fossil burrow systems. For example, *Palaeosabella prisca* (M'Coy) was originally referred to the sponge genus *Vioa*, then it became the type species of the worm genus *Palaeosabella*, and subsequently it has been suggested that it may be congeneric with *Topsentia devonica* Clarke, and should perhaps be relegated to the sponges (Teichert 1945).

Considering a hypothetical case, the present author would not be prepared to describe a new species of rabbit on the evidence of a fossil burrow in an Interglacial deposit! By analogy, it is not proposed to create new names for the burrows in the Cretaceous echinoid test. They are regarded as indications of the presence of organisms, but cannot be regarded as parts of organisms. The description of new species might be justified if the hypothetical rabbit burrow should subsequently yield bones, or if fossil burrows in shells and echinoids should yield spicules, chaetae, or other non-perishable parts. Otherwise, the system of letters used in the present description is adequate for reference purposes.

In conclusion, some of the burrows in the test of the Cretaceous echinoid indicate the probable presence of an echiuroid (C), a phoronid (D), and an acrothoracican cirripede (F), whereas the less distinctive burrows which allow more than one interpretation indicate the possible presence of a lamellibranch (B), polychaets and other 'worms' (B and E), and sponges (E and G).

I should like to thank Dr. C. F. A. Pantin for helpful discussion of the manuscript.

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WILKINGIA GEN. NOV. TO REPLACE *ALLORISMA* FOR A GENUS OF UPPER PALAEOZOIC LAMELLIBRANCHS

by R. B. WILSON

ABSTRACT. The Upper Palaeozoic lamellibranch genus *Allorisma* King 1844 is placed in the synonomy of *Edmondia* de Koninck 1842, as the type species, *Sanguinolaria sulcata* Phillips 1836, is conspecific with *Hiatella sulcata* Fleming 1828, the latter species being an *Edmondia*. The name *Allorisma* King 1850, for a sinu-pallial form, is replaced by the new name *Wilkingia*. The type species *Wilkingia* [*Venus*] *elliptica* (Phillips) is described.

THE author's revision of the Carboniferous lamellibranch species described by John Fleming (Wilson, *Bull. Geol. Surv. Gt. Brit.*, in press) has revealed that the surviving type specimens of *Hiatella sulcata* Fleming 1828, and *Sanguinolaria sulcata* Phillips 1836, are conspecific, and that the species should be assigned to *Edmondia* de Koninck 1842. On morphological grounds Fleming's original assignation of the species to *Hiatella* Daudin, a synonym of *Saxicava* Fleuriau, cannot be accepted. Of the original specimens named *Hiatella sulcata* by Fleming, seven still remain. Of these, one is selected as lectotype (Wilson, op. cit.); of the remainder three are indeterminable. Only one syntype of Phillips's species *Sanguinolaria sulcata* has survived. This specimen, although not Phillips's original figured specimen, was figured by Hind (1899, p. 321, pl. 34, fig. 3) as the probable type of Phillips's species. It has proved to be conspecific with the determinable syntypes of Fleming's species. *Hiatella sulcata* possesses well-developed internal cartilage plates and a non-sinuate pallial line, and has been assigned to *Edmondia* de Koninck. King (1844, p. 313) selected *Sanguinolaria sulcata* Phillips as the type species of his new genus *Allorisma*, emphasizing the presence of internal cartilage plates (fulcra) in the genus. Later, King (1850, p. 163) acknowledged the fact that de Koninck had already described these internal cartilage plates in *Edmondia*, and that species which he (King) had formerly placed in *Allorisma*, should be assigned to *Edmondia*. Unfortunately, he retained the name *Allorisma*, altering the diagnosis to include forms with a pallial sinus and without internal cartilage plates. For the modified genus he took *Hiatella sulcata* Fleming as type species, claiming that this species possessed a pallial sinus. The study of Fleming's specimens does not support this contention. To illustrate the genus, King (1850, pl. 20, fig. 5) figured a specimen possessing a pallial sinus which he called '*Allorisma sulcata* Fleming', but this specimen belonged to a species previously briefly described, figured and named *Venus elliptica* by Phillips (1836, p. 209, pl. 5, fig. 7). From morphological considerations, this form cannot be assigned to *Venus*, *Myacites* (Salter 1861, p. 221, pl. 1, fig. 28), or *Edmondia*, and as the name *Allorisma* is not available, it, and related species require to be grouped in a new genus for which the name *Wilkingia* is proposed, with *Wilkingia elliptica* (Phillips) here designated as type species.

Hind (1900, p. 422) recognized that the form King had figured as *Allorisma sulcata* was the same as that named *Venus elliptica*, but he used the name *Allorisma sulcata* for the species, as he considered that some examples of it were used by Fleming when describing *Hiatella sulcata*. The study of Fleming's syntypes does not support this view.

[Palaeontology, Vol. 1, Part 4, 1959, pp. 401–4, pl. 71, pars.]

Phillips (1836, p. 247) stated that the specimen he figured as *Venus elliptica*, here designated the lectotype of the species, was in the collection of the Yorkshire Philosophical Society, which is now housed in the Yorkshire Museum, York. The specimen cannot be found and is presumed lost. The specimen King (1850, pl. 20, fig. 5) figured as *Allorisma sulcata* is also missing. Unsuccessful searches for it have been made in the Hancock Museum, Newcastle upon Tyne, and University College, Galway, the two institutions in which it is most likely to have been preserved. The following descriptions are based on fourteen specimens in the collections of the Geological Survey and Museum, London, from Redesdale, Northumberland, which the author considers to be conspecific with *Venus elliptica* Phillips.

WILKINGIA gen. nov.

Type species *Venus elliptica* Phillips

Diagnosis. Elongate-oval lamellibranchs, equivalved, markedly inequilateral. Umbones placed far forward, their anterior border continuous with anterior margin of valve. Anterior and posterior extremities rounded, ventral margin gently convex, postero-dorsal edge straight or almost so. A broad, shallow sinus runs ventrally from the umbones in anterior half of valves. Escutcheon and elongate lunule present. Umbonal ridge poorly developed. Valves concentrically sulcate. Rows of small tubercles present, especially on postero-dorsal area. Adductor muscle scars shallow, pallial sinus present, hinge simple, probably edentulous.

Wilkingia elliptica (Phillips)

Plate 71, figs. 1–6

Venus elliptica Phillips 1836, p. 209, pl. 5, fig. 7.
? *Posidonomya transversa* Portlock 1843, p. 745, pl. 38, fig. 9.
Allorisma sulcata King 1850, pl. 20, fig. 5.

EXPLANATION OF PLATE 71

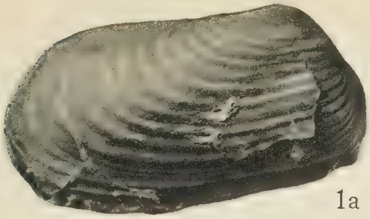
Figs. 1–6. *Wilkingia elliptica* (Phillips). All except figs. 3*b* and 4*b* are unretouched photographs, natural size. The specimens are in the Geological Survey and Museum, London. 1*a*, 14579, Redesdale, Northumberland, right valve, internal cast with part of original shell under umbo. 1*b*, Same specimen, dorsal view, showing lunule and elongate escutcheon. 2, Lectotype, reproduction of Phillips's original drawing of *Venus elliptica*, specimen lost. 3*a*, 14577, Redesdale, left valve, internal cast. 3*b*, Same specimen, part of pallial line and muscle scar as observed by author, drawn on photograph. 4*a*, 14586, Redesdale, right valve, internal cast. 4*b*, Same specimen, part of pallial line and muscle scar as observed by author, drawn on photograph. 5, 15823, Redesdale, right valve, internal cast of almost complete specimen. 6, 14582, Redesdale, left valve, internal cast showing rows of fine tubercles on postero-dorsal area.

Fig. 7. *Edmondia sulcata* (Fleming). Left valve of specimen in Hancock Museum, Newcastle upon Tyne, to show different ornament and shape of anterior from *Wilkingia elliptica*, × 1.

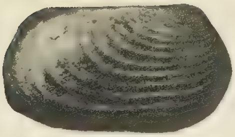
Figs. 8–10. *Posidoniella spp.* 8, 9, *P. vetusta* J. de C. Sowerby, Carboniferous Limestone Series. 8, British Museum (Natural History) PL. 357, ×1, Derbyshire. 9, PL. 803, ×1, the lectotype, Castleton, Derbyshire. 10, *P. variabilis* Hind, Millstone Grit Series, Manchester Museum L. 10227, ×2.

Figs. 11, 12. *Posidonia obliquata* (Brown), Millstone Grit Series, Lower *Reticuloceras* age, ×2.

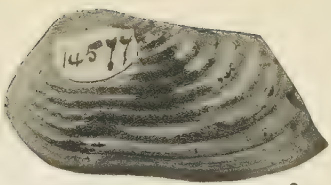
Figs. 13–15. *Caneyella spp.* 13, *C. richardsoni* Girty, reproduction of Girty 1909, pl. 4, fig. 1, Caney Shale, Oklahoma. 14, *C. membranacea* (M'Coy), ×1, Carboniferous Limestone Series, Upper *Posidonia* age. 15, *C. rugata* (Jackson), Millstone Grit Series, Upper *Reticuloceras* age, ×2.



1a



4a



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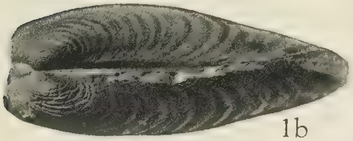
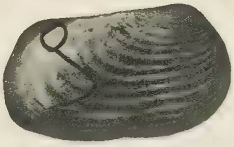


1b



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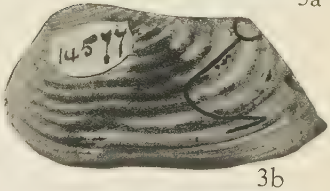

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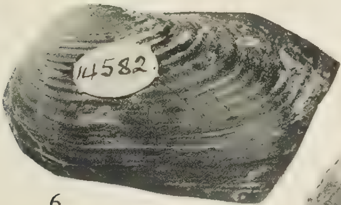

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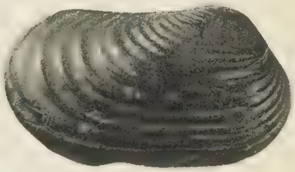

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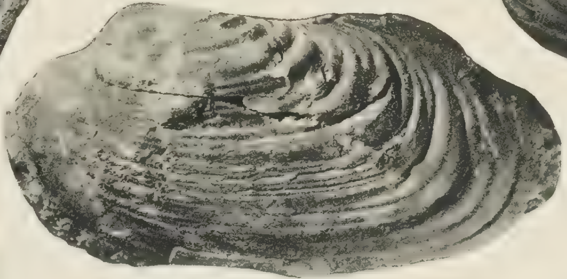

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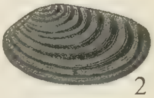
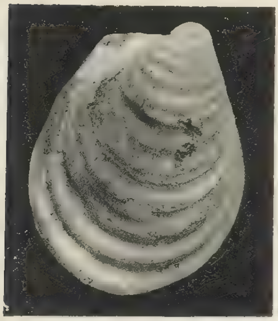


2



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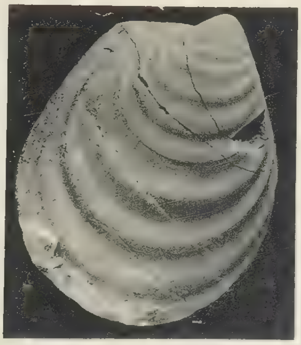

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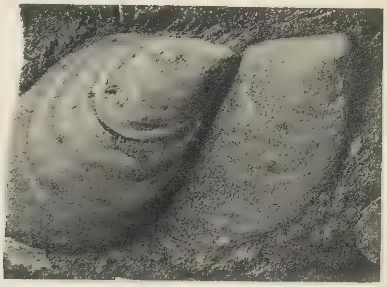
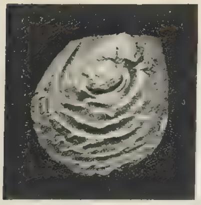
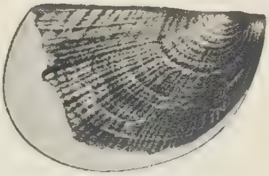


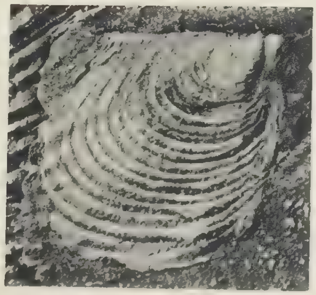
10 × 2



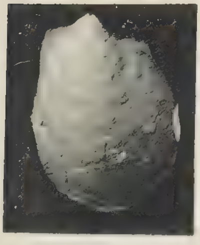
11 × 2



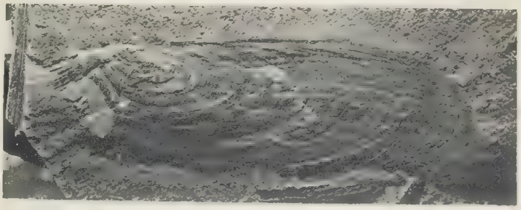
13 × 2



15 × 2



12 × 2



14

WILSON, *Wilkingia* gen. nov.
RAMSBOTTOM, Carboniferous Lamellibranchs

Sanguinolites sulcatus M'Coy 1855, p. 507.
Myacites sulcata Salter 1861, pl. 1, fig. 28.
Allorisma sulcata Hind 1900, pp. 422–4, pl. 48, figs. 3–11.

Lectotype. Specimen figured by Phillips (1836, pl. 5, fig. 7) from Northumberland, lost.

Description. Medium-sized, elongate-oval, length about twice height, anterior and posterior extremities rounded. Equivalved, markedly inequilateral, slight posterior gape. Umbones placed far forward, prosogyrous, raised above dorsal margin, their anterior margin continuous as a straight line with the upper part of the anterior border of the valves. Lower part of anterior margin of valves rounded, passing into gently convex ventral margin. Posterior border rounded, dorsal margin posterior to umbones almost straight, turned upwards slightly at posterior end. Maximum convexity of valves in umbonal region. A poorly developed, but definite shallow depression runs from the umbones towards the ventral margin, increasing in width in this direction. Umbonal ridges poorly developed, running towards and fading out about half-way to postero-ventral angle. Between umbonal ridges and dorsal margin, valves slightly concave. Lunule elongate, lanceolate, extending from umbones to anterior extremity of valves. Escutcheon elongate, narrow and deep, extending from umbones almost to postero-dorsal angle. Valves marked by non-bifurcating, prominent concentric ribs and grooves which stop at margins of lunule and escutcheon. In the postero-dorsal area, close-set rows of numerous small tubercles radiate from the umbones. Shell thin. Anterior adductor muscle scar not definitely observed but probably small and situated near anterior extremity of valve. Posterior adductor scar irregularly rounded, moderately large and situated under dorsal margin near posterior end. Deep sinus in pallial line present, but only seen on exceptionally well-preserved specimens. Ligament external, hinge line not seen but probably edentulous.

Dimensions of figured specimens (in mm.). Figures followed by (E) are estimated from incomplete specimens.

	Length	*Height*	*Width*
14577 (Pl. 71, figs. 3*a*, *b*)	44(E)	22	14
14579 (Pl. 71, figs. 1*a*, *b*)	50(E)	27(E)	17·5
14582 (Pl. 71, fig. 6)	53(E)	27	18
14586 (Pl. 71, figs. 4*a*, *b*)	33	17	11·5
15823 (Pl. 71, fig. 5)	42(E)	22	14
Lectotype, measured from Phillips's drawing (Pl. 71, fig. 2)	20	10·5	. .

Discussion. The horizon and locality of the lectotype are not known, Phillips (1836, p. 209) giving only Northumberland as the locality. The specimen probably came from the old workings in the Redesdale Ironstone, of Lower Carboniferous age, Redesdale, Northumberland. King's figured specimen, and the specimens used here to describe the species, are from this locality. Although the postero-dorsal outline of Phillips's drawing is not typical of specimens here regarded as belonging to the same species, such an outline has been observed on specimens where this part of the shell is incomplete. A specimen from Fermanagh, crushed and incomplete, figured as *Posidonomya transversa* by Portlock (1843, pl. 38, fig. 9), may belong to the present species.

Much has been written concerning the presence of a pallial sinus in the species. King (1850, pl. 20, fig. 5) showed a sinus to be present, but M'Coy (1855, p. 276) denied that such a character existed, and placed the species in *Sanguinolites* (op. cit., p. 507). Hind (1896, p. 25) also doubted its presence, stating that the line was drawn in ink on King's figured specimen. Hind (1900, p. 424) later changed his opinion, claiming that a pallial sinus was present, and figured specimens showing the feature (1900, pl. 48, figs. 3, 4, 8). An examination of these specimens in the British Museum (Natural History) showed that the pallial line is drawn in pencil on two of the specimens, presumably as a guide to the artist, and is not obvious in the third specimen. As the issue still appeared to be in doubt, a collection of specimens which had never been figured was studied. Of the fourteen specimens examined, the writer is convinced that two of them show undoubted evidence of a pallial sinus. These are figured (Pl. 71, figs. 3*a*, 4*a*) as unretouched photographs and also (Pl. 71, figs. 3*b*, 4*b*) with the pallial sinus drawn in to show its position. The feature is only visible on very well-preserved specimens, and even then can only be seen satisfactorily under magnification.

Hind (1899, pp. 320–1; 1900, pp. 423–4) discussed the differences between the present species and *Edmondia sulcata* (Fleming) which bears a superficial resemblance to it. A specimen of the latter species is figured (Pl. 71, fig. 7) to show how the ribs on *E. sulcata* split into finer ones as they cross the centre of the valve, and how the outline in front of the umbones is concave, two points which easily distinguish it from *Wilkingia elliptica*. Further points of difference, although not always seen, are that *E. sulcata* has an entire pallial line and had well-developed internal cartilage plates. Although both species are elongate-oval with prominent concentric ribs, they probably occupied different ecological stations. *W. elliptica*, with its posterior gape and pallial sinus, was presumably a burrower and *E. sulcata* perhaps led a more active existence.

Acknowledgements. The writer is indebted to the Directors of the British Museum (Natural History) and of the Geological Survey and Museum, the late Mr. C. E. Fisher of the Hancock Museum, Newcastle upon Tyne, Professor J. Mitchell of University College, Galway, and Mr. G. F. Willmot of the Yorkshire Museum, York, for access to, and information concerning, the collections in their care, and to Dr. W. H. C. Ramsbottom for advice during the course of the work. This paper is published with the permission of the Director of the Geological Survey of Great Britain.

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NOTES

DISTINCTIONS BETWEEN THE CARBONIFEROUS LAMELLIBRANCH GENERA *CANEYELLA*, *POSIDONIA*, AND *POSIDONIELLA*

by W. H. C. RAMSBOTTOM

EXAMPLES of lamellibranchs variously referred to the genera *Posidonia* and *Posidoniella* occur abundantly in the Viséan and Namurian rocks of England. This note gives external characters by which the two genera may be distinguished from each other and from the genus *Caneyella*. It is published with the permission of the Director of the Geological Survey of Great Britain.

POSIDONIELLA de Koninck 1885

Type species by monotypy: *Inoceramus vetustus* J. de C. Sowerby 1829, p. 162, pl. 584, fig. 2. Two specimens, now in the British Museum (Natural History), were figured by Sowerby, of which the original of the upper figure is now No. PL. 804, and that of the lower figure PL. 803. The latter is here designated lectotype, and figured on Pl. 71, fig. 9, it comes from Castleton, Derbyshire. PL. 804 is from 'near Settle', Yorkshire. The horizon of both specimens is probably B_2 zone of the Lower Carboniferous.

Remarks. In this genus the umbo is terminal and the hinge, though not clearly seen, is apparently not striate and is edentulous, and in these features the genus differs from *Myalina*. The terminal umbo distinguishes this genus from both *Posidonia* and *Caneyella*, and places the genus in the Myalinidae, in contrast to *Posidonia* and *Caneyella* which are Pectinids.

Of the British Millstone Grit species which have been referred to this genus, only *P. variabilis* Hind and forms determined as *P.* cf. *vetusta* are correctly placed here. In *P. rugata* Jackson 1927, *P. multirugata* Jackson 1927, and *P. semisulcata* Hind, the umbo is not terminal and they are here referred to *Caneyella*. *Caneyella wapanuckensis* Girty from the Caney Shale of Oklahoma apparently included at least two species. No lectotype has been chosen. Girty's fig. 9 is very like *P. variabilis* Hind, and his figs. 6, 7, and 11 are reminiscent of *Posidonia corrugata* R. Etheridge jun. Examples of the type species of *Posidoniella* and of *P. variabilis* Hind (lectotype here chosen the original of Hind 1897, pl. 7, fig. 7, Manchester Museum L. 10227) are figured on Pl. 71.

POSIDONIA Bronn 1828

Type species by monotypy: *P. becheri* Bronn 1828, pp. 262–9, pl. 2, from the Lower Carboniferous near Herborn, Germany. In Britain *P. becheri* is most abundant in rocks of Lower *Posidonia* (P_1) age, but allies occur in the B_2 zone and it has been reported in P_2.

Remarks. Weigelt (1922) considered *Posidonia* and *Caneyella* to be synonymous, but Newell (1938, p. 37) doubted the propriety of placing *Caneyella*, judged on its costate type species 'with the noncostate and otherwise quite different *Posidonia*'. The type species of the two genera, *P. becheri* and *C. richardsoni*, represent two extreme forms between which there are so many intermediates that it is difficult to draw up satisfactory diagnoses. The following scheme, however, seems to be workable.

Posidonia is here restricted to noncostate species in which the umbo is more or less centrally placed on the relatively short hinge-line, or at least not less than one-third of the length of the hinge-line from the anterior end. *Caneyella*, as here restricted, includes both costate and a few noncostate species with a relatively long hinge-line, the umbo being usually towards the anterior end. These distinctions, when applied to adult shells, seems to have genetic significance and to separate shells which are not congeneric.

In the British Carboniferous *Posidonia* is represented by *P. becheri* (most common in the P_1 zone); *P. corrugata* and its allies, some of which are undescribed, ranging from P_2 to E_2; *P. obliquata* Brown in R_1 and possibly R_2 zones; *P. insignis* (Jackson) in G_1, and *P. gibsoni* in G_2. The well-known *P. membranacea* M'Coy (Pl. 71, fig. 14) is transferred to *Caneyella*.

CANEYELLA Girty 1909

Type species by original designation: *C. richardsoni* Girty 1909, pp. 38–39, pl. 4, figs. 1, 1*a*, Caney Shale, Oklahoma. Elias (1956, pp. 66–67) gives the horizon as the Delaware Creek member, the goniatite fauna of which is evidently of Lower Carboniferous *Posidonia* Age, possibly P_2.

Remarks. Distinction of this genus from *Posidonia* has been given above. Bisat (1924) commented that *C. richardsoni* resembled *Actinopteria* cf. *persulcata* (M'Coy) as found in the Bowland Shales of England. There is a difference, however, in that the growth lines on the posterior part of the shell as they approach the hinge-line in adult *Caneyella* bend back towards the umbo, whereas in *Actinopteria* they bend away from the umbo and form an incipient wing. Young examples of *Caneyella* may show a wing.

Of the species which Girty (1909) referred to *Caneyella* it is proposed that *C. nasuta* Girty be suppressed as a subjective synonym of *Caneyella* [*Posidonia*] *membranacea* (M'Coy), and *C. vaughani* Girty be suppressed as a subjective synonym of *Posidonia becheri* Bronn. Other species of the genus occurring in the British Carboniferous include *C.* [*Posidoniella*] *semisulcata* (Hind) in the *Homoceras* zone, *C.* [*Posidoniella*] *rugata* (Jackson) in the Upper *Reticuloceras* zone, and *C.* [*Posidoniella*] *multirugata* (Jackson) in the *Gastrioceras* zone.

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A NEW LIASSIC DRAGONFLY FROM GLOUCESTERSHIRE

by F. E. ZEUNER

THE dragonflies of the Lias are of great phylogenetic interest as evolution was at that time very rapid. It is worth while, therefore, to describe a new form from Cheltenham, Gloucestershire.

The specimen is a hindwing of a *Progonophlebia*, larger than the species described by Tillyard in 1925.

Progonophlebia cromptoni sp. nov.

Plate 72, fig. 4

Diagnosis. A *Progonophlebia* with wings approximately 43 mm. long.

Distribution. Lower Lias, Cheltenham, Gloucestershire.

Holotype. British Museum (Natural History), In. 49297, G. E. Gavey Collection, presented by Rev. J. Crompton, May 1956.

Parts known. Hindwing.

Description. To facilitate comparison, I am following Tillyard's wording and terminology closely (Tillyard 1925), although I do not agree with his interpretation of the venation.

Costal space crossed by two strongly formed antenodals, one on either side of the arculus. Nodus placed about half-way along the costal margin, and formed by the subcosta running into the costal margin with a slight bend upwards, and supported below, just before the actual apex of Sc, by a cross-vein, at the lower end of which R bends obliquely downwards for a very short distance, and then turns to run straight below C, giving off a very strong cross-vein placed slightly obliquely, which is the subnodus. Postnodals few in number. Pterostigma of moderate length, enclosed by oblique cross-veins, which are more distal on the Sc than on the R and curved, with their concavity towards the base of the wing. M_1 slightly converging with R towards the pterostigma. M_{1A} rootless and converging with M_1 in the apex. M_2 arising distad of the subnodus, being separated from it by almost two complete inter-cross-vein spaces. This is characteristic of *Progonophlebia*. M_S arising from a cross-vein placed in the angle between M_{1+2} and M_3, and separated from both by only one row of cells. M_2, M_S, and M_3 terminate close together far distad along the wing in the apex. M_4 slightly zigzagged in the middle of its course, though less so than in *P. woodwardi* Till. It continues to do so toward its end, where it converges with Cu_1. Cu_1 well developed, but not stronger than the other longitudinal veins. Cu_2 weak, disappearing in the network of cells. Discoidal cell undivided, longer than wide (shorter in *P. woodwardi*). Anal portion of wing missing. Length 43·5 mm. (apex damaged); maximum width 11·2 mm.

Remarks. The agreement with *Progonophlebia woodwardi* Till. is so close that there can be no doubt about the generic identity. Several details are included in the description which are not available in Tillyard's species. The chief difference between *P. woodwardi* and *P. cromptoni* is that the latter is much longer, the total length being 43·5 instead of only 35 mm. The other specific differences are in the shape of M_4 and the discoidal cell, and in slight deviations of the courses of the veins from the picture presented by Tillyard (1925, fig. 1). These are characteristically differences on the species level. Two species of *Progonophlebia*, therefore, visited the coastal regions of the British Lias, just as there are several species of *Libellula* to be observed on ponds at the present day.

REFERENCE

TILLYARD, R. J. 1925. *The British Liassic Dragonflies.* London, Brit. Mus. (Nat. Hist.).

JURASSIC BEETLES FROM GRAHAMLAND, ANTARCTICA

by F. E. ZEUNER

THE Falkland Islands Dependencies Geological Survey has produced a few remains of fossil insects from Mount Flora, Hope Bay, Grahamland, Antarctica. In view of the locality alone these specimens are of considerable interest, though from the point of view of classification they will remain somewhat obscure until more material has been assembled. They were collected by the late Mr. W. N. Croft of the British Museum (Natural History) in 1946.

Four beetle elytra belonging to at least two different species are preserved in a piece of black shale (with counterpart). They are associated with numerous unidentifiable fragments of plants. One of the elytra shows evidence of prolonged soaking in water, the others look fresh and appear to have been thicker. One is fragmented (In. 51767), and there are some unidentifiable traces of insect legs. The concentration of the specimens in one layer and on a small piece of shale measuring 4×4 in. suggests that this is a potentially prolific locality for fossil insects. On the other hand, the insect remains appear to have drifted about in water, so that mainly detached wings and legs are likely to be found if further collecting is undertaken. In any case, they are not abundant in all horizons, for Dr. Mary Calder has not found other insect remains among the plant specimens she is studying from the same locality. The late Mr. W. N. Edwards inclined to the view that the plant remains on the slab under discussion may be rootlets.

Locality: Mount Flora, Grahamland, 25 feet below top of plant horizon, 25 yards west of the Arête, altitude *c.* 1175 feet, No. D. 37. 15. *Types.* British Museum (Natural History), nos. given below.

Grahamelytron crofti gen. et sp. nov.

Plate 72, figs. 1, 2

Holotype. In. 51764, Pl. 72, fig. 1, with counterpart. *Paratype.* In. 51765, Pl. 72, fig. 2, with counterpart. *Size.* Elytron (holotype): length 11·5 mm., width 4·8 mm.

Description. The external margin forms a narrow, slightly upturned flange. There are fifteen longitudinal grooves separating slight 'ridges'. Of the latter every second bears small tubercles, which are especially pronounced in the distal portion. These may be due to the internal structure of the elytron and they need not have been apparent in life. In this case, the elytron would have offered a smooth external appearance with fifteen fine grooves. The alternative of external tubercles cannot however be ruled out. In any case the tuberculate ridges are wider than the intermediate ones. The fusion of the grooves and ridges at the apex of the elytron is obscured in the holotype by folds due to softening in water.

The holotype is a left elytron, and the paratype is a right one. Its basal portion is missing, 7 mm. being preserved. Its measurable width, 4·6 mm., agrees closely with that of the holotype, and it lies in close proximity to it. The two therefore are likely to have formed a pair, coming from the same individual. The number of grooves is the same, and the tubercles are well preserved (fig. 2). Again, the tuberculate ridges are wider than the smooth ones.

Interpretation. The structure of the elytron of this species, which is being dedicated to the memory of the late W. N. Croft of the British Museum (Natural History), is not inconsistent with that of certain Carabidae, for instance *Calosoma*, in which genus a similarly large number of grooves is present. Most other genera have fewer. A fossil genus that has a similar number of rows of tubercles is *Mesosagrites* Martynov (1935) from the Mesozoic of Cheliabinsk. Moreover, it resembles the Antarctic fossil in shape. *Mesosagrites multipunctatus* Martynov, which

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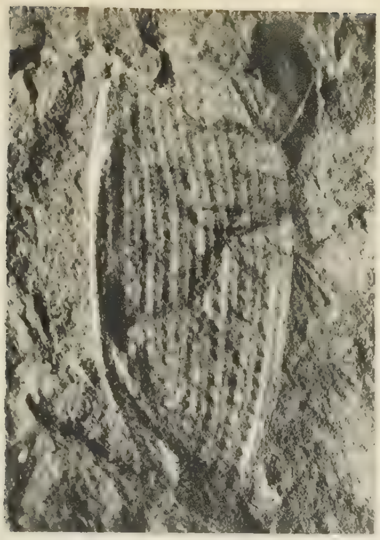
EXPLANATION OF PLATE 72

Figs. 1, 2. *Grahamelytron crofti* gen. et sp. nov., Mount Flora, Grahamland, Antarctica. 1*a*, *b*, Holotype and counterpart, In. 51764, ×5·5. 2*a*, *b*, Paratype and counterpart, In. 51765, ×7.

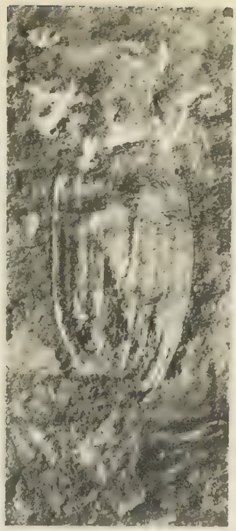
Fig. 3. *Ademosynoides antarctica* sp. nov., Mount Flora, Grahamland, Antarctica. Holotype, In. 51766, ×8.

Fig. 4. *Progonophlebia cromptoni* sp. nov., Lias, Cheltenham, Gloucestershire. Holotype, In. 49297, ×1·9.

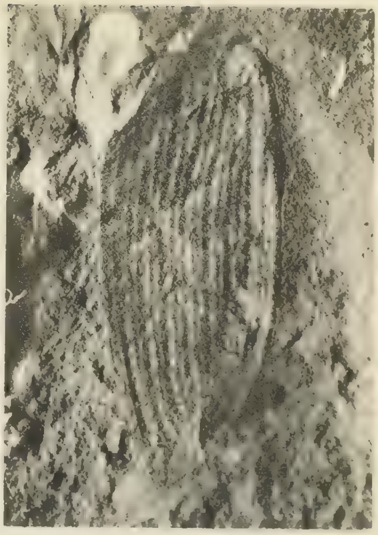
The specimens are in the British Museum (Natural History).



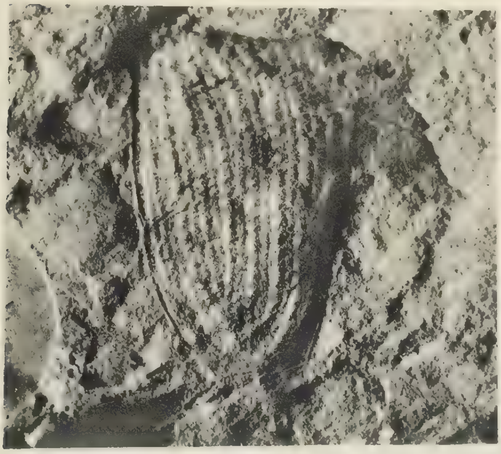
1a × 5.5



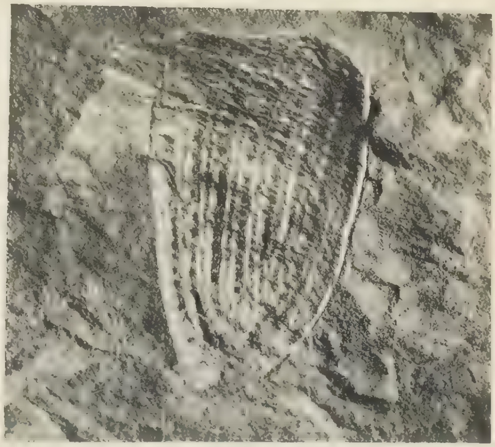
3 × 8



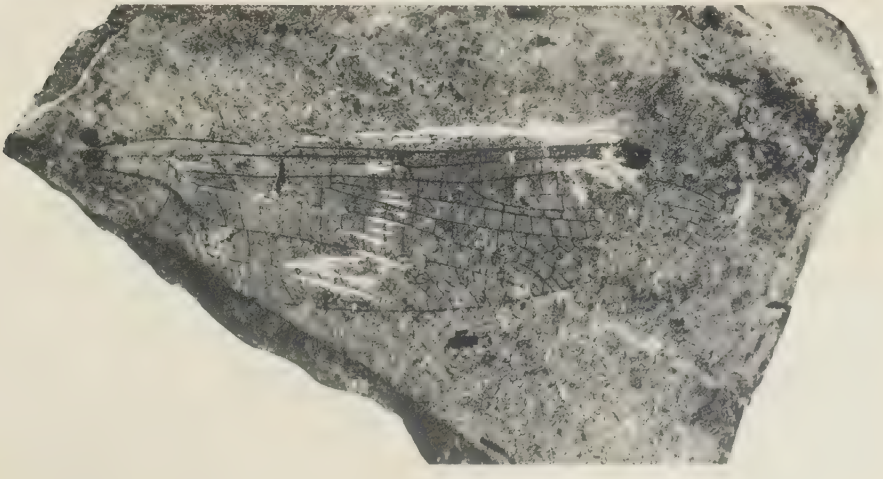
1b × 5.5



2a × 7



2b × 7



4 × 1.9

ZEUNER, Jurassic insects

agrees closely in size with *Grahamelytron*, was placed in the Chrysomelidae by its describer and particularly in the group around the genus *Sagra* Fabr. Martynov considers that the larvae may have lived in shallow water on plants. Whilst the present writer hesitates to assume close relationship between *Grahamelytron* and *Mesosagrites*, and to accept their assignment to the Chrysomelidae, it is noteworthy that *Mesosagrites* is 'not younger than Middle Jurassic, but more probably Liassic'. This agrees well with the 'Jurassic age' of the Mount Flora shales.

Ademosynoides antarctica sp. nov.

Plate 72, fig. 3

Holotype. In. 51766.

Size. Left elytron, length *c.* 4 mm. (3·3 mm. preserved), width 2·3 mm.

Description. Smaller than *Grahamelytron*. Surface smoother. Nine very fine grooves are present, and a narrow flange. No other sculptured features can be recognized. The proximal margin of the specimen is covered by rock which cannot be removed.

Interpretation. The writer finds it difficult to assign this fossil to a particular family, though circumstantial evidence is suggestive. To begin with, all families with specialized elytra can be ruled out. But it is conceivable that the fossil belongs, for instance, to the Carabidae, the Tenebrionidae (known from the Triassic, Zeuner 1930), or the Elateridae.

There is, however, an extinct family which requires careful consideration. These are the Permosynidae established by Tillyard in 1924 for beetles from the Upper Triassic of Belmont, New South Wales. *Permosyne* Tillyard is replaced by *Ademosyne* Handlirsch (1909) and *Ademosynoides* Dunstan in other localities, ranging from Narellan, New South Wales, to Ipswich in Queensland. Finally, *Ademosynoides asiaticus* Martynov (1936) was described from the Kuznetzk Basin in Russia. All these localities are of Triassic, and the Australian ones of Upper Triassic age.

Of these genera the fossil most resembles *Ademosynoides*, especially in the striae, and it is for this reason tentatively placed here. The resemblance to an Australian group of Triassic beetles is perhaps more than fortuitous.

Long ago, Handlirsch made an attempt to place *Ademosyne*. He concluded that this genus was related to the Recent Hydrophylidae, which are also known with certainty from the Tertiary (Zeuner 1938). This family leads an aquatic life, and if Handlirsch's view applies to the Permosynidae as a whole, this would be consistent with the nature of the shales of Mount Flora, indicating shallow fresh water with plenty of plant growth in and around it.

Conclusion. Both *Grahamelytron crofti* and *Ademosynoides antarctica* suggest an Upper Triassic to Jurassic age of the Mount Flora Beds, and this confirms the views of the palaeobotanists who regard the plants as Middle Jurassic. Biologically both can be referred to groups living in fresh water. Palaeogeographically, a connexion with Australia is indicated.

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MARTYNOV, A. V. 1935. Zametka ob iskopoemych nasekomych iz mesosoickich otlozhenii čelyabinckogo burouglonovo basseina. *Trud. paleozool. Inst. Akad. Nauk S.S.S.R.*, **4**, 37–48.

—— 1936. O nekotorych novych materialach clenistonogich zhivotynych iz kuznetskogo basseina. *Izv. Akad. Nauk S.S.S.R., Sci. nat.* 1936, 1252–64.

TILLYARD, R. J. 1924. Upper Permian Coleoptera and a new order from the Belmont Beds, New South Wales. *Proc. Linn. Soc. New South Wales*, 1924, 429.

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THE PALAEONTOLOGICAL ASSOCIATION

Extracts from the Annual Report of the Council for 1957

FOUNDATION. The formation of a Palaeontological Association was first discussed at a palaeontological dining club which began meeting in London late in 1954. At a meeting on 21 November 1956 a committee was elected, and Dr. R. G. S. Hudson was invited to become its chairman; the composition of the committee was: Dr. R. G. S. Hudson, Dr. F. Hodson, Mr. N. F. Hughes, Dr. W. S. McKerrow, Dr. W. H. C. Ramsbottom, Dr. J. T. Temple, and Dr. Gwyn Thomas. At a later date Professor Alwyn Williams was co-opted. The Committee was instructed to consider the ways and means of founding a Palaeontological Association, to obtain estimates of the cost of publishing a journal, to submit proposals for a constitution, and to call a meeting in January 1957. On 1 January 1957 a first circular was issued. It outlined proposals for the formation of an Association, and contained an invitation to a public meeting to be held in the Royal School of Mines, London, on 30 January 1957. Seventy persons attended this meeting. Dr. Hudson, who was in the chair, outlined the need for a Palaeontological Association. Mr. N. F. Hughes, acting as spokesman for the committee, explained the proposals which had been put forward. It was announced that a second meeting would be held formally to inaugurate the Association, adopt a constitution, elect a Council and empower it to collect subscriptions. A discussion ensued concerning the name and aims of the proposed Association, its relationships with existing societies, the holding of meetings, and the financial aspects of establishing a new journal. A resolution, proposed by Dr. E. I. White and seconded by Dr. F. W. Anderson, 'that an Association to further the study of palaeontology be formed' was carried unanimously. A second resolution, proposed by Mr. R. V. Melville and seconded by Professor O. M. B. Bulman and Mr. W. S. Bisat, 'that Dr. Hodson, Dr. Hudson, Mr. Hughes, Dr. McKerrow, Dr. Ramsbottom, Dr. Temple, Dr. Gwyn Thomas, and Professor A. Williams are elected as an organizing committee, and are requested to report progress at a meeting to be called in the near future' was carried unanimously.

The second circular, distributed on 13 February, announced the inaugural meeting of the proposed new Association to be held in the Royal School of Mines on 27 February 1957. At this meeting, attended by forty-nine persons, a constitution was discussed and accepted. The following were then elected as Officers and Council of 'The Palaeontological Association' for 1957: *President*: Dr. R. G. S. Hudson. *Vice-Presidents*: Dr. E. I. White, Mr. N. F. Hughes. *Treasurer*: Dr. W. S. McKerrow. *Editor*: Dr. W. H. C. Ramsbottom. *Secretary*: Dr. F. Hodson. *Fourteen other members of Council*: Dr. F. W. Anderson, Dr. T. Barnard, Professor O. M. B. Bulman, Dr. F. E. Eames, Mr. G. F. Elliott, Professor T. N. George, Dr. Dorothy H. Rayner, Mr. P. C. Sylvester-Bradley, Dr. J. T. Temple, Dr. Gwyn Thomas, Professor T. S. Westoll, Professor W. F. Whittard, Professor Alwyn Williams, and Professor Alan Wood. It was resolved that the Council be authorized to publish a journal and that the Officers of the Association be authorized to act as an Executive Committee of the Council.

The first Council meeting was held at the Geological Survey and Museum on 1 May 1957. Finance, publication, and meetings sub-committees were established. Appeals for funds had already been initiated. It was agreed that the name of the journal should be '*Palaeontology*', that initially two parts a year should be published, that it should be crown quarto in size, and that it should be printed by the Oxford University Press. At the second Council meeting on 29 June the Council accepted with regret the resignation of Dr. Hodson as Secretary, and recorded its thanks to him. Dr. Gwyn Thomas was elected to fill the vacancy.

MEMBERSHIP. On 31 December 1957 there were 372 members.

FINANCE. The accounts and balance sheet for 1957 are given below. The donations resulting from the appeals campaign have been placed in a Foundation Fund. Most of the donations are the first of three annual payments. The Council wishes to thank the managements of the Companies concerned for their valued support and generosity.

'PALAEONTOLOGY'. Volume 1, part 1, containing 7 papers and consisting of 86 pages and 14 plates was published in November.

MEETINGS. The first Demonstration Meeting was held on 29 June at Bedford College, London. There were fifteen exhibitors, each of whom briefly described his exhibit. The first Discussion Meeting was held in the Department of Geology, the University of Sheffield, on 13–14 December. The subject was 'Carboniferous Zonal Stratigraphy' and five papers were read at each of two sessions.

OVERSEAS REPRESENTATIVES. The following have agreed to serve as overseas representatives of the Association: *Australia*: Dr. Dorothy Hill. *New Zealand*: Dr. D. A. Brown. *West Indies and Central America*: Dr. L. J. Chubb. *Canada*: Dr. D. J. McLaren. *Eastern U.S.A.*: Professor H. B. Whittington. *Western U.S.A.*: Dr. J. Wyatt Durham.

DELEGATE. Dr. R. G. S. Hudson was elected as the Association's representative on the newly-formed Geological Conservation Council, and was appointed its chairman.

ACCOUNTS FOR YEAR ENDING 31 DECEMBER 1957

General Account

Income	£	*s.*	*d.*	*Expenditure*	£	*s.*	*d.*
Members' subscriptions . .	723	16	10	*Palaeontology*	610	12	8
Sale to non-member . . .	1	3	6	Office expenses	69	3	5
Interest	11	14	3	Surplus of general income over expenditure	56	18	6
	£736	14	7		£736	14	7

Foundation Fund

Donations	£	*s.*	*d.*
Professor O. M. B. Bulman . . .	1	1	0
Attock Oil Company	50	0	0
Ultramar Company	50	0	0
Apex (Trinidad) Oilfields . . .	50	0	0
Iraq Petroleum Company . . .	300	0	0
Imperial Chemical Industries . . .	25	0	0
Shell Petroleum Company . . .	250	0	0
	£726	1	0

Balance Sheet

Liabilities	£	*s.*	*d.*	*Assets*	£	*s.*	*d.*
Surplus of general income over expenditure	56	18	6	Barclays Bank Current Account .	740	7	10
Balance of Foundation Fund . .	726	1	0	Barclays Bank Deposit Account .	661	14	3
					1,402	2	1
				Less cheques in transit . .	619	2	7
	£782	19	6		£782	19	6

Auditors: J. M. Edmonds, H. G. Reading

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